TALL EUCALYPT FORESTS OF AUSTRALIA: STRUCTURE, PATTERN AND PROCESS

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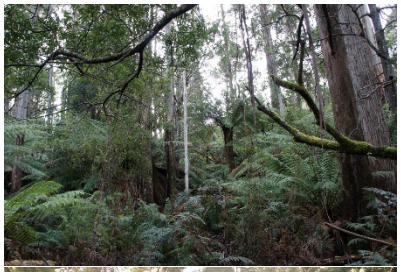
Thesis submitted in fulfilment of the requirements for the

Degree of *Doctor of Philosophy*

Submitted June, 2017



DECLARATION

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STATEMENT OF ETHICAL CONDUCT

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

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STATEMENT OF PUBLISHED WORK

Candidate was the primary author on all chapters, undertook substantial fieldwork, and did most data analyses. For each respective chapter, the candidate as well as all co-authors contributed to developing the ideas. Barry W. Brook and Nicole Bezemer assisted with the field work – collecting fallen wood and topographic data that contributed to Chapters III, VI, VIII and IX. David M. J. S. Bowman provided access to the primary data used in Chapters III, IV, VI, VII and IX. Barry W. Brook, Stefania Ondei, George P. W. Perry, John Alroy, Andrew Cole and John Dickey contributed to some data analysis. The candidate as well as Barry W. Brook assisted with refining the text.

Supplementary Information for all chapters, including data and additional analyses, can be found here: https://ecological-dynamics.org/data/

The following papers have resulted from this Ph.D. thesis research:

Buettel, J.C., Bowman, D.M.J.S., Perry, G.L.W., Hovenden, M.J. & Brook, B.W. (2016) A global synthesis of reported spatial patterns in forests. *Ecography* (in review).

Buettel, J.C., Perry, G.W.P., Ondei, S. & Brook B.W. (2017) Drivers of spatial pattern, density and basal area in Australian tall eucalypt forests. *Journal of Ecology* (in review).

Buettel, J.C., Alroy, J. & Brook, B.W. (2017) Latitudinal controls on forest species richness are not direct. *Nature Ecology and Evolution* (in review).

Buettel, J.C., Ondei, S. & Brook, B.W. (2017) Look down to see what's up: A systematic overview of treefall dynamics in forests. *Forests* **8**, 123. doi:10.3390/f8040123.

Buettel, J.C., Ondei, S., Dickey, J.M., Cole, A.A. & Brook, B.W. (2017) Reading the forest logbook: environmental drivers of living and dead elements of Australian eucalypt forests. *Diversity and Distributions* (in review).

Buettel, J.C., Ondei, S. & Brook, B.W. (2017) Missing the wood for the trees? New ideas on defining forests and forest degradation. *Rethinking Ecology* (in press). doi: 10.3897/rethinkingecology.@.13296

Buettel, J.C., Ondei, S. & Brook, B.W. (2017) A practical method for creating a digital topographic surface for ecological plots using ground-based measurements. *Landscape Ecology* (in review).

Buettel, J.C., Cole, A., Dickey, J.M. & Brook, B.W. (2017) Modelling linear spatial features in ecology. *Ecology* (in review).

Buettel, J. C., Brook, B.W., Cole, A.A., Dickey, J.M. & Flies, E.J. (2017) Interdisciplinary to transdisciplinary: shifting the collaboration paradigm for greater advances in science. *Ecology and Evolution*. (in review).

Buettel, J.C. & Brook, B.W. (2016) Egress! How technophilia can reinforce biophilia to improve ecological restoration. *Restoration Ecology* **24**, 843-847. doi: 10.1111/rec.12387 (article featured on the journal cover).

Additional publications candidate co-authored during PhD:

Brook, B.W. & **Buettel, J.C.** (2016) Emigration is costly but immigration has benefits in human-altered landscapes. *Functional Ecology* **30**, 1478-1479. doi: 10.1111/1365-2435.12639.

Brook, B.W., Ellis, E.C. & **Buettel, J.C.** (2017) What is the evidence for planetary tipping points? Chapter 8 in: *Effective Conservation Science: Data Not Dogma* (eds. P. Kareiva, M. Marvier & B. Silliman), Oxford University Press (in press). ISBN: 9780198808985.

Johnson, C. N., Balmford, A., Brook, B.W., **Buettel, J.C**., Galetti, M., Guangchun, L. & Wilmshurst, J.M. (2017) Biodiversity losses and conservation responses in the Anthropocene. *Science* **356**, 270-275 (major review). doi: 10.1126/science.aam9317.

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ACKNOWLEDGEMENTS

There are many people that have been part of my journey these last 3.5 years, and the stress of forgetting anyone is almost equivalent to 'waiting for the in-review status to change to awaiting editor decision for a manuscript submission!' So, I will start by offering a sincere thank you to everyone that has had an impact on my PhD at any stage throughout my journey – you *may* not have been mentioned in these acknowledgments but be rest assured that my bad memory is the reason!

I would, first and foremost like to give a wholehearted thank you to my supervisor Barry Brook, for taking me under his wing and providing me with ample opportunities to grow and excel. There was never a challenge he thought I couldn't rise to; his constant belief in my ability, and support and encouragement that he provided will remain with me for the rest of my career. I am proud, and sincerely blessed to have been under his tutelage.

My PhD would not have been possible without the AusPlots data and David Bowman's belief that I would be able to do it justice. TERN (AusPlots), Sam Wood, Karl Rann and everyone associated with the funding and collection of these data – I am deeply grateful.

A massive thank you to Nicole Bezemer for her dedication and help with field work. We created some great memories on those trips.

John Dickey and Andrew Cole – thank you for your enthusiasm and willingness to dabble in ecology, and providing me with support and encouragement along the way. I never thought I would have had such stimulating conservations about the analogies between galaxies (stars) and ecology (trees).

Jon, I am deeply grateful for your friendship, guidance and support throughout this journey, I could not have done it without you.

I also wish to thank my close friends and family for their support and patience throughout this journey. My family's mantra: 'you are Jessie Buettel and you can do anything,' is a perfect testament to their unwavering belief in me.

Stefania Ondei, you are amazing. That is all.

To the D.E.E.P lab – I appreciate your patience and encouragement during my PhD completion. You are a wonderful and fun group of people.

Sam Adlard, Ian Cover, Emily Flies, thank you for being there for me and believing in me – particularly through all the tough times.

A warm thanks to Scott Carver, Vector, Relly, (the puppas) and Lynx for being my rock(s) through turbulent times, and having such a positive influence on my life. Scott, I also would not have gotten through my Ph.D. without a coffee machine – best gift EVER!

I would also like to acknowledge the support of the Australian Postgraduate Award scholarship and the Multidisciplinary Environment Research Group (MERG) for providing financial support for myself and my innovative research endeavours.

Many people have kindly given their time to help improve both the written and intellectual elements of this dissertation – finally, to all co-authors, many thanks!

SUMMARY

The use of observed patterns to infer underlying biotic and physical drivers of eco-evolutionary dynamics is a challenge for population, community and conservation ecology. This is because whilst an understanding of process is required to make useful predictions and test theory, it is static or progressive patterns that are most readily observed in ecological systems, especially at landscape scales. In this thesis, I report on the links between pattern and process, using spatially explicit plot-based information from 48, one hectare tall eucalypt forest communities, spanning the coastal zones of eastern, southern and western Australia. These data are the first to be established across a continental Australian forest system, and were analysed using a combination of point-pattern statistics, likelihood-based inference, structural equation modelling, and simulation modelling. I also developed two new methods for analysing landscape topography and mapping the spatial location of treefalls. Interdisciplinary collaborations, including with astrophysicists, underpinned the novelty of the research. I demonstrated that, at a local scale, climate was a strong predictor of non-eucalypt basal area and density, and eucalypt basal area (but not density), consistently explaining >40% of the deviance in these variables. While non-eucalypts thrived within narrower temperature ranges (indicating avoidance of temperature extremes), eucalypt density and basal area were higher in cold-dry conditions. Regional-to-continental-level analyses revealed that community diversity and carbon storage were decoupled in Australia, the former being driven largely by biogeographic factors and the latter by latitudinal gradients and evapotranspiration. This decoupling was not evident for the global forest biomes, supporting the assertion that Australia's eucalypt forests are unique – in the context of the tall forest biome – in a global context. The

findings from this thesis underpins, both theoretically and empirically, the fundamental processes influencing forest structure and function in the tall eucalypt forests of Australia. For management and conservation to be successful in today's human-dominated 'Anthropocene', a thorough process-based understanding of the ecosystem in question is required. In the case of Australian tall eucalypt forests, I show how thinking outside-the-box, measuring treefall, engaging in interdisciplinary collaborations, and facilitating innovative solutions, are a productive way forward.

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CHAPTER I

INTRODUCTION TO PATTERN AND PROCESS IN FOREST ECOLOGY

Forests are complex three-dimensional ecosystems whose structure and function are shaped by biotic (living: plants, animals, micro-organisms) and abiotic (non-living: environmental, physical) components. An overarching aim of forest ecology is to isolate and understand each component, so as to build a picture of how they are interrelated, and how they shape overall ecosystem function in synergy. In this introductory chapter, I overview the main processes that influence forest structure, describe how forest patterns develop and are maintained through time, and briefly explore the methods currently used in forest-ecology research. I also introduce the principal dataset used in this study (AusPlots), and describe the aims and key questions that are explored and addressed throughout the remainder of this thesis.

Forests are the dominant land-based ecosystem worldwide by area, sequester almost half of the planet's terrestrial surface carbon, and regulate climate at local to global scales (Pan *et al.* 2013a). Projected pressures due to global change, including expansion of agriculture and biofuels, forestry, and climate-driven shifts, pose significant threats to global forest biodiversity, structure and function (Meyfroidt *et al.* 2010). Understanding how these pressures and threats might manifest over time is critical, particularly in the context of the conservation of these natural ecosystems. Ultimately, ecological processes such as succession, climate, plant-plant interactions, disturbance (fire, windthrow), decomposition, turnover, and nutrient availability and dynamics, are essential to the development of forest pattern (Fig. 1; Buettel *et al.* 2017). This spatial patterning and structure is further characterised by horizontal (niche differentiation, resource and water availability), and vertical (tree height, canopy, light availability) elements of variation, and it is the differences in these factors that give rise to complex forest structures (Franklin *et al.* 2002b). Pinpointing the underlying mechanisms that drive forest structure and tree distribution—that is, linking observed patterns to underlying processes—is key to predicting how forest dynamics will respond to disturbance and global change, given underlying differences in climate, species composition and distribution.

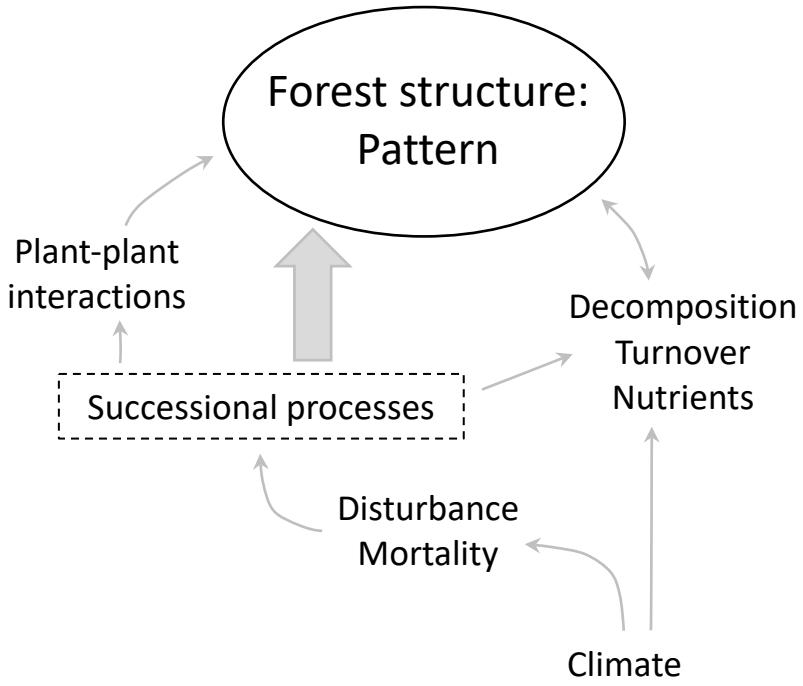


Fig. 1: *Factors (processes) that influence forest pattern, and how they are interrelated*. Successional processes are a central feature that determines the 'state' and age of the forest (i.e., along a continuum from young and regenerating to old and 'stable') and is influenced by, and related to, all biotic and abiotic processes mentioned above.

Development of forest pattern

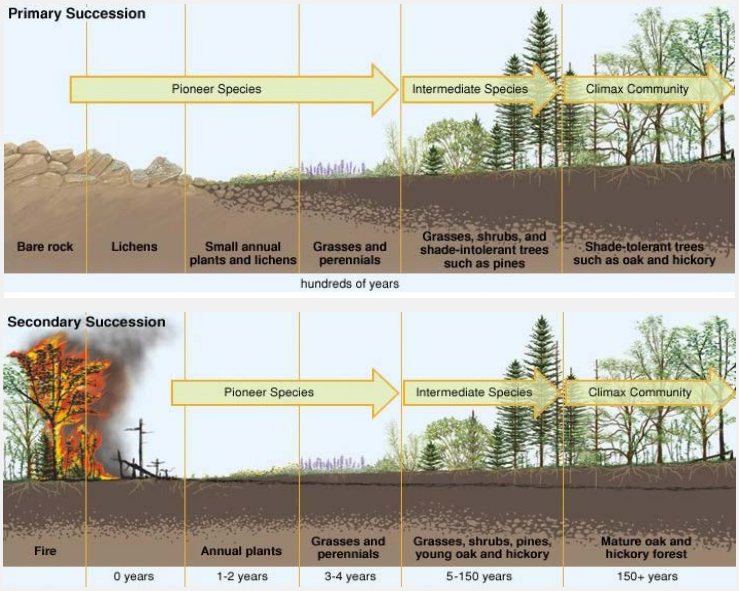
Successional processes/forest age

Stand structure and forest composition is often conceptualised as a sequence of temporal snap-shots of ongoing primary or secondary successional processes (Box 1; Chen *et al.* 2004). In reality, successional processes create a continually shifting composition of species within the community, fluctuating as disturbances of different intensities, sizes and frequencies alter the landscape. The serial progression of tree species depicted in Box 1 is not random; certain species have evolved life histories to exploit the conditions that define each successional stage. As environmental

conditions and disturbance frequencies change, a partially predictable sequence of habitats is created in which only a narrow suite of species can thrive (West *et al.* 2012). Once established, the residing species can alter key processes such as light intensity on the forest floor, soil composition, and the availability of nutrients in the environment, to ensure successional process (tree replacement) continues. In some environments, succession reaches a climax, which is characterised by a small number of dominant species that form a stable community, whilst in others, disturbance is a persistent feature that continually creates a flux of species diversity. Throughout this research thesis, I focus largely on communities that are in 'dynamic equilibrium' (i.e., consist of a diverse mix of species, including numerous mature trees, but experience continual small- to large-scale disturbances), and are dominated by a single genus, *Eucalyptus*.

Box 1: ***Primary and secondary succession***

Primary succession occurs from a baseline environment devoid of visible life. Environments are typified by soil or rock that has been impacted by, for example, lava flows, newly formed sand dunes or rock remaining from a retreating glacier.



Box 1 figures: Two types of successional processes a) primary succession and b) secondary succession. Source: Encyclopaedia Britannica (http://britannica.com/)

Secondary succession occurs from a baseline of pre-existing life and nutrients that have been temporarily removed, either through small- to large-scale disturbances that retain environment functionality.

Forest age, or time since last disturbance, is an important attribute of forest structure and succession as it influences size and density of the component species and the availability of resources like nutrients and light. Consequently, many deterministic processes during stand structural development, such as net primary production (NPP), mortality, biomass, and woody debris accumulation, are related to stand age (Spies 1998). Early successional forests have a higher proportion of fast-growing species and higher mortality rates due to intense competition for light and space among rapidly growing trees (Enquist and Niklas 2002). Therefore, these forests can achieve high woody productivity but relatively low wood density and biomass. In contrast, forests in later successional, or "old-growth" stages, are typified by a shade-tolerant

understory with a canopy of larger species that may have had relatively fast growth rates before reaching crown maturity, and decreased biomass growth after canopy closure (Ryan *et al.* 2004). By maintaining slow growth and low mortality on relatively nutrient-poor soils, these trees may survive for centuries and achieve a high biomass (Pan *et al.* 2013b). Consequently, each tree species within a forest is likely to exhibit a range of spatial patterns depending on the successional stage. Determining the frequency, intensity and duration of the processes that generate these patterns is essential for understanding how forest patterns develop over time..

Climate

Climate contributes significantly to macro-scale patterns in forest productivity, with temperature, rainfall and solar radiation all imposing a strong constraint on plant physiological processes and growth (Coomes *et al.* 2014). Plant physiological responses, especially to changes in climate, are highly dependent on site-specific factors that limit forest growth. As a result, the interplay between the environment, habitat suitability and resource availability, are important for governing the distribution of plant species. However, while general plant physiological responses to changing climate are well documented (Coomes *et al.* 2014), specific responses to climate also depend on factors such as species composition, diversity and tree density. For example, forests growing in warmer regions often have a well-developed understory of shade-tolerant species, and this strongly influences light interception and stand productivity (Coomes and Grubb 2000; Morin *et al.* 2011). Similarly, species within highly diverse forest stands have been shown to exhibit an 'additive basal area', using both above- and below-ground resources more effectively and leading to greater wood production (Paquette and Messier 2011; Vilà *et al.* 2013). As species shift their

distributions to occupy suitable climates, new forest communities assemble (Bertrand *et al.* 2011; Zhu *et al.* 2012; Coomes *et al.* 2014). Therefore, climate is considered a strong predictor of current and future plant distributions, growth and forest structure.

Decomposition, turnover and nutrients

The availability of nutrients within an ecosystem depends on the input and efficient cycling of nutrients within and across communities (Prescott 2002). There are multiple pathways through which this is achieved: plant to soil, soil to plant (root uptake) and internal redistribution of nutrients (Sharma and Sharma 2004). Plants return nutrients to the soil as litter, comprising a mixture of fine (leaf litter, bark, twigs) and course material (branches and fallen trees), which are decomposed (Sharma and Sharma 2004). Decomposition and turnover are critical determinants of the global carbon cycle and nutrient turnover (Del Grosso *et al.* 2005; Parton *et al.* 2007), and are therefore paramount in shaping forest structure and pattern.

Fallen wood is critical to site fertility and productivity, acting as a long-term sink for nutrients through the process of decomposition (Harmon *et al.* 1986). It is also one of the few forest attributes that can act as a feedback mechanism (Fig. 1), whereby changes in decomposition rates, and thus nutrient release, can impact forest structure and composition. Consequently, any change in forest structure will drive decomposition and turnover, and create cyclic feedbacks. This internal dynamic is also influenced by temperature, moisture, and the stage of decay of the woody debris (Laiho and Prescott 2004). For example, a recently fallen tree contains many readily available nutrients, and as decay proceeds, its moisture-holding capacity increases, but its nutrients are steadily depleted. Furthermore, attributes of the woody debris and its

surrounding environment, such as chemical properties (determined in part by species identity), size, mode of death, microclimate, biotic community are collectively important for determining rates of turnover, decomposition and nutrient release in forests (Buettel *et al.* 2017). Understanding the properties and the spatial distribution of fallen wood may indeed be key to unlocking further information about forest structure and process.

Disturbance and mortality

The presence of fallen wood, fire scars on trees and position of standing dead trees are important indicators of disturbance and/or mortality. Such events are often unpredictable, random (i.e., not 'set' in to the usual time sequence of succession), hard to detect, and can often vary in scale (i.e., impact individuals to communities to landscapes). However, their presence and location in the forest community, if measured, can be used to infer information about past processes.

Aside from minor fluctuations over periods of time, in say, the mortality rate among old trees, there are factors of rare or sporadic occurrence, such as fire, storms and drought, which may cause a stand-replacing event or, more commonly, create 'gaps' in the landscape or canopy. In forest gaps, recruitment occurs (due to optimal climate and resources for example), and a cohort of trees establish. These newly emerged trees will persist and grow, eventually die, and all the while exerting a strong influence on the structure of the forest into the next generation (Wiens 2007). This is an example of how a sporadic disturbance and mortality event (such as tree-fall) may influence the patterns observed in plant communities which, over time, leaves lasting changes (legacy effects) in the landscape (within the area of influence). These disturbance

patterns, alongside information of the living tree community, can be used to monitor the health of a forest community, and aid in the detection of forest ecological processes.

Plant-Plant Interactions

Local interaction among trees can have a strong influence on the emergent community structure in forests, and through plant competition, can create distinct hierarchies of horizontal and vertical structure in forest stands (Franklin *et al.* 2002a). In a resource-limited, highly competitive systems, two contrasting types of biological interaction prevail: repulsion and attraction (Stoyan and Penttinen 2000). Repulsion is a 'negative' ecological interaction and is mainly caused by strong inter- and intra-specific competition. Mortality-driven repulsion leads to regular spatial distributions of trees. The spatial scale of these negative interactions is a good indication of the extent to which competition is influencing the spatial distribution of plants. Conversely, attraction is a 'positive' interaction that leads to aggregation or clumped distributions within plant communities. These distributions are typically due to limitations in dispersal, vegetative reproduction or facilitation at a local scale (Callaway and Walker 1997). The strength of interactions between individual plants, and the outcome of these for the spatial distribution of trees within a forest, are important means through which to infer dynamic ecological processes from static patterns.

Current ecological methods

Spatial point pattern analysis – the traditional 'top-down' approach

One of the most common and straightforward methods for determining the type of biological interaction occurring within forest systems is to examine the spatial locations of individuals. The underlying spatial pattern of a forest community may conserve and reveal an imprint of past processes, constituting an 'ecological archive' from which we may recover information of the underlying processes (Wiegand and Moloney 2013). Quantifying and determining the underlying processes responsible for spatial patterns of ecological phenomena has been addressed using experimentation, direct parameterisation of spatial models from data, simulation of processes within a spatial domain, and through analysis of the spatial pattern itself (McIntire and Fajardo 2009b, Brown *et al.* 2011). The statistics of spatial distribution on a landscape, such as Ripley's *K*, pair correlation function or the distribution of the nearest neighbour distances, are used to quantify small-scale spatial correlation structures of a pattern which contains information on the positive or negative interactions among plants, depending on proximity (Wiegand and Moloney 2013).

Studies that have examined the spatial patterning of plant communities have demonstrated that non-random patterns prevail, particularly in shrubland and tropical rainforest systems (Perry *et al.* 2008). This research highlights that the main driving force of the observed aggregation or regularity of plant spatial patterns is through strong intra- and inter-specific competition, species co-existence mechanisms and dispersal limitation (see section 2.3). Studies such as these, however, rarely go beyond the initial univariate (pattern of one individual population/species) or bivariate analyses (pattern between two [potentially interacting] groups). Consequently, the relative contribution of different processes that might be generating the patterns observed usually remain obscure and not easily defined, making inference in these

complex systems difficult (McIntire and Fajardo 2009a). Arguably, embracing a detailed description of space requires more empirical data, that permits a narrower focus on specific questions within a single ecosystem. No one approach to capturing spatially structured interactions is likely to be adequate for all ecosystems, but determining the appropriate level of detail is an important step in understanding the influence of spatial interactions on emergent community structure.

Those plant distributions that are apparently random, as distinct from clustered or regular, indicate either an absence of significant spatial interaction or a temporal transition from negative to positive interactions, or vice versa (Wiegand *et al.* 2000). Therefore, characterising the type of biological interaction is important for determining the strength of competition between individuals and the factors that shape their distribution within communities and across the landscape.

Simulation modelling – a 'bottom-up' approach

There are many types of simulation modelling in ecology, ranging from simple to highly complex, depending on data and purpose. A simulation model of a forest might start in some simple form and incorporate only a select few variables (e.g., recruitment, growth and mortality). As understanding of the ecosystem deepens, so too does the opportunity to elaborate and further parameterise the model (e.g., by including more variables like climate, disturbance frequency). Such models are thus often built from the 'bottom-up' (i.e., by simulating the underlying processes and interactions, to reproduce observed patterns), with the goal of understanding and forecasting forest dynamics. Simulation models allow researchers to examine the sensitivity of tree populations or the forest community to the strength of different processes, to test

plausible ranges for parameters (e.g., demographic rates and competition coefficients), examine importance of initial conditions in succession and equilibrium states, and to test the impact of events/trends like fire, storms (stochastic) and climate change or logging (deterministic) pressures. Two types of simulation modelling common in landscape or conservation ecology are gridded/lattice and agent-based models (McGlade 2009).

A gridded model is designed to represent static and dynamic attributes at the grid/cell scale, and a description of how individual grid cells interact with their surrounds and other biological or physical properties of the environment (spatial relationships) (e.g., Karafyllidis and Thanailakis 1997; Cannas *et al.* 1999; Tonini *et al.* 2014). Attributes can be represented as scalars, vectors, matrices or other higher-dimensional structures (Nakamaru 2006). Spatial variation is captured via a lattice of cells, connected by adjacent borders and potentially also interconnected by multi-cell step processes (e.g., long-distance dispersal) or cascading effects transmitted from cell to cell (Hogeweg 1988). Processes (which might interact) are captured by mathematical and operational rules that dictate how attributes vary, both within a given grid cell and across spatially distributed cells. These processes also impose how attributes respond to change over time, or how they are distributed in space. Patterns, both aspatial (e.g., size distributions, density, diversity, etc.) and spatial (e.g., point-pattern statistics, patchiness, fractal dimensions) 'emerge' from the model, bottom-up, as a result of the application of processes to attributes, and might be related complexly due to feedbacks and synergies. Agent-based models (ABMs), a special class of individual-based models (IBMs), are similar to gridded models, but can be represented by continuous space (McGlade 2009), where individuals (trees) are modelled as autonomous agents

that interact and follow 'decision rules' (Macal and North 2010). ABMs remove the need to select specific values for each parameter of interest; rather, these seek to capture the diversity of attributes and behaviours that exist for each 'agent' and observe how patterns arise through their interactions (DeAngelis and Grimm 2013). Such an approach offers the prospect of new insights into forest dynamics (Railsback and Grimm 2011), by observing how patterns change over time depending on the 'agents' within the forest community of interest.

Many forest-dynamics models have already been developed, dating back over four decades, and include: JABOWA (the original "gap-phase replacement" model; DeAngelis and Grimm 2013), TROLL (a 3-D model of Neotropical plants; Chave 1999), BEFORE (a grid-based model of northern beech-forests; Rademacher *et al.* 2004), FLAMES (simulating the spatial response of eucalypt-savanna trees to fire disturbance; Liedloff and Cook 2007) and SORTIE (sortie-nd.org). These are largely site-specific, and are of varying complexity.

AusPlots permanent forest plot network

To study forest dynamics, plot-based censuses of individual trees have been undertaken in many regions, in pursuit of an idiosyncratic mix of inventories, surveys, experimental treatments and long-term repeated sampling, to monitor changes in tree distribution, carbon storage and mortality—sometimes spanning decades of observations at a given site. Such permanent-plot networks can also yield important ecological insights over the short term. For example, they offer the tantalising prospect of inferring life-cycle processes and forest structure (e.g., Fig. 1) from 'snap-shot'

studies of tree locations, sizes, and species identity, based on the idea that the spatial pattern of trees might conserve the fingerprints of past, often hidden, processes (Wiegand and Moloney 2004; Perry *et al.* 2013).

My research thesis (specifically Chapters II, IV, V, VI, VIII, IX), was based on analysis and modelling of data collected from a permanent plot network that was established for Australia in 2012–2014, via the Terrestrial Ecosystems Research Network (TERN) funded "AusPlots" project (ausplots.org), along with new fieldwork done by me at a dozen of these sites in 2015–2016. This monitoring programme involved the establishment of 48 × 1-hectare plots situated in tall-eucalypt forests of Australia, stratified across the continent (Fig. 2), with all individual trees (>10 cm diameter at breast height; DBH) identified to the species level and mapped by their spatial coordinates and size. The AusPlots data, which being so recent has not yet been interrogated in any scientific detail (Wood *et al.* 2015), provided an ideal foundation for the detailed analysis and modelling of pattern and ecological process in Australian eucalypt systems. Globally, it is now the most extensive standardised forest-plot network with explicit spatial information within any single forest type.

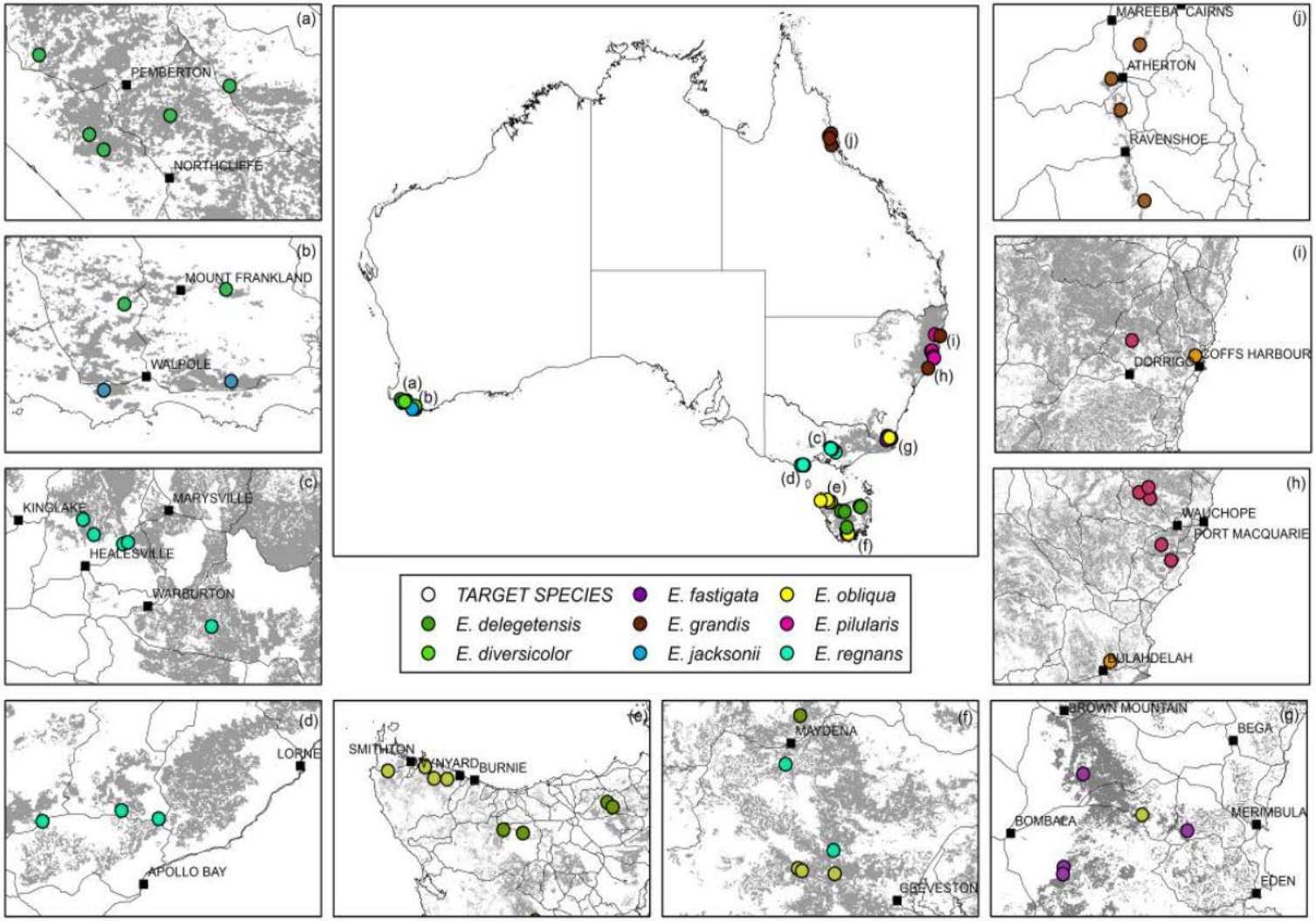


Figure 2: Map of the AusPlots permanent plot network (Adapted from; Wood *et al.* 2015). The small frames surrounding the map of Australia show the locations of each plot within each geographic region (Queensland, New South Wales, Tasmania, Victoria and Western Australia).

Table 1: Key ecological features in the AusPlots tall eucalypt forest network. Ni = number of individuals, Ns = number of species, Nd = number of standing dead trees, Elev = elevation, Asp = aspect, MAT = mean annual precipitation (mm), MAP = mean annual precipitation)

State	Habitat	Plot ID	N*i*	N*s*	Dominant species	N*d*	Elev	Asp	MAT	MAP	Latitude	Longitude
WA	Seasonal	Carey	118	3	*E. diversicolor*	13	164	S	15.3	1098	-34.3866	115.8457
WA	Seasonal	Dombakup	292	5	*E. diversicolor*	20	93	S	15.2	1163	-34.5764	115.9829
WA	Seasonal	Warren	148	3	*E. diversicolor*	6	134	N	14.8	1175	-34.5459	115.9522
WA	Seasonal	Dawson	165	4	*E. diversicolor*	38	148	N	15.2	1105	-34.8497	116.6872
WA	Seasonal	Giants	261	5	*E. jacksonii*	27	158	S	15.1	1132	-34.9805	116.8793
WA	Seasonal	Sutton	110	4	*E. diversicolor*	46	142	N	15	1006	-34.4488	116.2498
WA	Seasonal	Frankland	192	4	*E. diversicolor*	3	239	S	14.8	1026	-34.8247	116.87
WA	Seasonal	Clare	253	4	*E. jacksonii*	4	165	N	15	1204	-34.9954	116.6504
WA	Seasonal	Collins	117	3	*E. diversicolor*	13	136	S	14.9	1120	-34.5078	116.1242
NNSW	Tropical-subtropical	Mines Rd	275	16	*E. pilularis*	136	535	N	15.4	1434	-31.2803	152.5368
NNSW	Tropical-subtropical	A-Tree	451	10	*E. pilularis*	64	631	N	15.3	1375	-31.2421	152.4609
NNSW	Tropical-subtropical	Tinebank	484	14	*E. pilularis*	46	600	S	16.2	1362	-31.2086	152.5267
NNSW	Tropical-subtropical	Lorne	396	21	*E. pilularis*	113	283	S	16.5	1457	-31.5828	152.6164
NNSW	Tropical-subtropical	Bird Tree	612	21	*E. pilularis*	77	352	N	16.1	1542	-31.6858	152.6825
NNSW	Tropical-subtropical	Black Bull	376	13	*E. pilularis*	42	683	S	15.5	1895	-30.1578	152.727
NNSW	Tropical-subtropical	Bruxner	868	40	*E. grandis*	101	188	S	18	1872	-30.2401	153.0918
NNSW	Tropical-subtropical	OSullivans	546	21	*E. grandis*	50	75	S	17.6	1323	-32.3455	152.2605
QLD	Tropical-subtropical	Mt Baldy	196	29	*E. grandis*	52	1058	S	19.4	1326	-17.2698	145.4187
QLD	Tropical-subtropical	Herberton	237	3	*E. grandis*	35	1048	N	18.9	1601	-17.1107	145.5609
QLD	Tropical-subtropical	Lamb Range	271	14	*E. grandis*	92	1148	N	19.4	1376	-17.4158	145.4644
QLD	Tropical-subtropical	Koombaloomba	391	25	*E. grandis*	118	795	N	20.5	1732	-17.8416	145.5843

State	Habitat	Plot ID	N*i*	N*s*	Dominant species	N*d*	Elev	Asp	MAT	MAP	Latitude	Longitude
VIC	Temperate	ANU101	248	7	*E. regnans*	120	337	N	11.2	1502	-37.5308	145.5167
VIC	Temperate	Ada	425	10	*E. regnans*	220	784	S	10.3	1714	-37.8049	145.8672
VIC	Temperate	Weeaproinah	799	9	*E. regnans*	122	471	N	11.2	1869	-38.6437	143.4749
VIC	Temperate	Turtons Rd	490	10	*E. regnans*	40	480	S	11.1	1654	-38.639	143.7014
VIC	Temperate	Lardners Rd	531	8	*E. regnans*	49	531	N	11.3	1701	-38.6238	143.629
VIC	Temperate	ANU363	123	3	*E. regnans*	85	580	N	11.7	1445	-37.5936	145.6263
VIC	Temperate	ANU589	316	7	*E. regnans*	81	579	S	11.6	1468	-37.5893	145.6396
VIC	Temperate	HardyCreek	216	8	*E. regnans*	191	830	N	10.5	1641	-37.5693	145.5465
SNSW	Temperate	Newline	310	6	*E. fastigata*	51	955	S	10	853	-36.7591	149.4351
SNSW	Temperate	Waratah Mix	270	6	*E. fastigata*	26	828	N	10.4	917	-36.9969	149.3821
SNSW	Temperate	Wog Way	215	6	*E. fastigata*	32	845	S	10.9	911	-37.014	149.3808
SNSW	Temperate	Goodenia	158	8	*E. fastigata*	31	420	N	13.1	1000	-36.9035	149.7176
SNSW	Temperate	Candelo	154	7	*E. fastigata*	32	645	N	11.9	953	-36.8631	149.5949
TAS	Temperate	Flowerdale	379	9	*E. obliqua*	69	206	N	11.4	1406	-41.0449	145.5661
TAS	Temperate	Dip River	679	7	*E. obliqua*	59	247	N	11.2	1477	-41.0345	145.4055
TAS	Temperate	McKenzie	480	11	*E. delegatensis*	129	790	S	7.5	1723	-41.6303	146.2593
TAS	Temperate	Caveside	1577	11	*E. delegatensis*	124	691	N	7.4	1368	-41.6697	146.5007
TAS	Temperate	Bird Track	496	13	*E. obliqua*	84	212	S	10.3	1466	-43.0891	146.6435
TAS	Temperate	Supersite	416	12	*E. obliqua*	118	111	S	11.2	1364	-43.0953	146.6551
TAS	Temperate	North Styx	473	11	*E. regnans*	82	560	S	9.7	1299	-42.8118	146.6083
TAS	Temperate	Weld	287	10	*E. regnans*	66	87	S	11	1228	-43.0411	146.7435
TAS	Temperate	ZigZag	1028	9	*E. obliqua*	137	284	N	10.2	1381	-43.1028	146.7472
TAS	Temperate	Mt Field	677	13	*E. delegatensis*	108	843	S	6.6	1309	-42.6829	146.6492
TAS	Temperate	Black River	553	8	*E. obliqua*	93	49	S	12.4	1139	-40.9525	154.2852
TAS	Temperate	Bond Tier	528	10	*E. obliqua*	25	54	S	12.3	1275	-40.9526	144.842
TAS	Temperate	Mt Maurice	430	10	*E. delegatensis*	117	752	N	8.7	1371	-41.3113	147.5383
TAS	Temperate	Ben Ridge	560	6	*E. delegatensis*	97	910	S	8.6	1350	-41.3673	147.6025

Thesis aims

There are many gaps in knowledge and unsolved topics in forest ecology, that are centred on the importance of the processes underpinning observed spatial patterns. Furthermore, beyond description, there are relatively few applications of hypothesis- and process-driven (bottom-up) mechanistic models and frameworks to answer critical questions on the future of Australia's tall-eucalypt forests: a biome under pressure from both global change and local anthropogenic pressures. Therefore, my thesis focuses on developing—for the first time—a comprehensive understanding of the structural and spatial processes that govern tall eucalypt forests across Australia, with the goal of deriving generalities that provide both a useful contribution to ecological theory, and practical benefits for the conservation of these spectacular Australian ecosystems (Fig. 3).

Overview of thesis chapters:

A further 11 chapters follow this general *Introduction* (I). The experimental chapters of this thesis (Chapters II, IV, V, VI, VIII, IX) have utilised the AusPlots forests database. Chapters II and IV are global analyses. Chapters V and VII are reviews that were pivotal to establishing the direction of my research. Chapters VIII and IX are methodological innovations that I conceived and developed during my candidature. Chapters XI and XII are case studies showcasing how I have been able to apply my conceptual findings to highlight new areas of research and public engagement. All subsequent chapters are either accepted or in-review in refereed journals, but have been re-formatted for this thesis (including figure and table numbering), with the references and supplementary material combined into a single end section. In all cases I was lead author, and developed and conducted the research under the guidance of

my supervisors. Due to the paper-style structure of this thesis, some repetition of concepts and ideas, especially in the Introduction and Discussion sections of papers, was unavoidable.

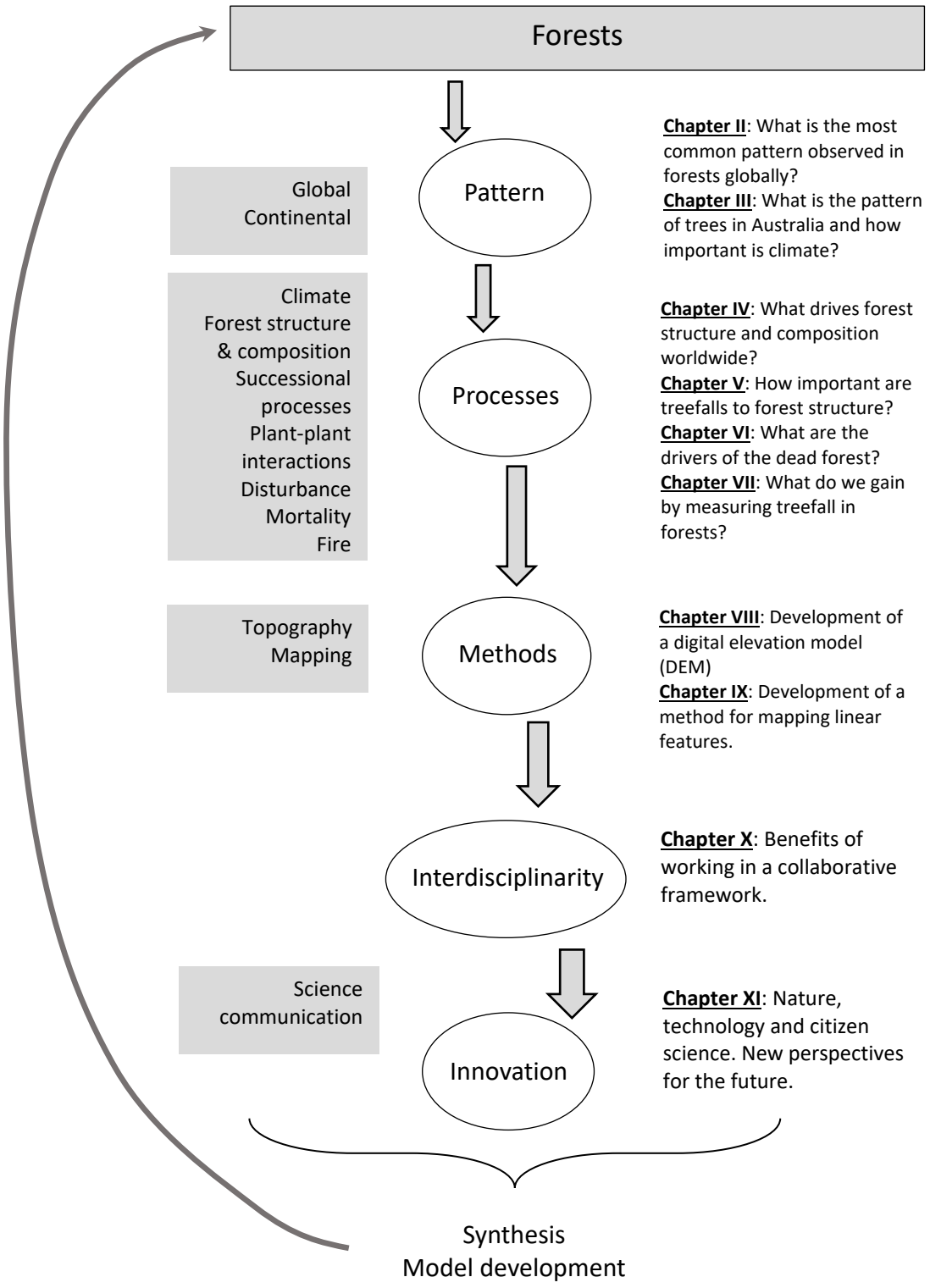


Fig. 3: Overarching thesis structure and framework. The arrows show the flow of idea generation, and the natural sequence of research.

CHAPTER II

A GLOBAL SYNTHESIS OF REPORTED SPATIAL PATTERNS IN FORESTS

Studies on large tropical forest plots suggest that aggregation is a common pattern for trees. However, despite the sophisticated tools available to analyze spatial information, it remains unclear whether plot design and/or geographic location of forest plots that report spatial information are globally cross-comparable. We synthesized the spatially explicit forest-plot data from six continents, based on the 87 studies reporting explicit pattern statistics (either as community composites or for individual species). From these, 264 unique forest plots, including >1,000 species occurrences, were represented. Our analyses demonstrated that aggregation is not a tropical peculiarity; it persists as the dominant pattern (over 65% of communities and species) reported in forest-plots worldwide. However, our ability to synthesize reported global pattern data and generalize across studies was confounded by differences in the number of species analysed per plot, geographical bias across continental forest areas, and methodological inconsistencies (in plot size and minimum size of individual trees measured). Researchers are likely to continue to

place a strong emphasis on point-pattern statistics for characterizing spatial structure. For these data are to be included in future meta-analyses, we recommend a more standardized approach to reporting metrics, and coordination of the choice of plot and tree size measured.

Introduction

The desire to improve understanding of forest dynamics and structuring has led to the widespread adoption of plot-based censuses of individual trees around the world (Anderson-Teixeira *et al.* 2015). These studies use a combination of static-pattern measurements and long-term monitoring to follow changes in tree distribution, carbon allocation, mortality etc., over time. The baseline data for these permanent plot networks is usually a 'snap-shot' study of tree locations of one or more species within the community, typically established with the underlying goal of deducing past processes from observable standing patterns (Perry *et al.* 2002; Wiegand and Moloney 2004). However, interpreting these instantaneous spatial data and linking it to time-dependent ecological processes is inferentially challenging (McIntire and Fajardo 2009), especially during periods of rapid environmental change. For instance, despite the availability of robust methods for analysing spatial point-patterns, there remains a wide range of simple to complex metrics and model outputs that are being reported (Velázquez *et al.* 2016). This has meant that, to date, few generalities or convincing syntheses have emerged on any reciprocal link between pattern and process in forest dynamics (Grimm *et al.* 2005).

Ideally, connecting an observed spatial pattern to a specific process should follow from a detailed plot-based analysis of local attributes such as topography, disturbance, and legacy effects (a 'bottom up' approach), although such studies are rare (Grimm *et al.* 2005; McIntire and Fajardo 2009). By contrast, the forest-ecology literature is replete with plot studies across most continents and biomes, testing for patterns of trees at the regional or local scales using stochastic spatial point-process models; the most common null expectation is complete spatial randomness (CSR). Such null models are typically used as a point of reference to contrast structure in pattern (e.g., aggregation, regularity) or randomness (Pielou 1960). However, it is widely recognized that the scale of analysis is critical for determining underlying processes that lead to spatial structuring, with most research suggesting that aggregation is typical in tropical forest plots at distances <30 m (Plotkin *et al.* 2002; Wiegand *et al.* 2007; Cheng *et al.* 2014). Explanations for this local aggregation tend to draw on species biology (such as growth rate, tree size, density, dispersal and competition) (Seidler and Plotkin 2006; Murrell 2009; Nakagawa *et al.* 2015), environmental heterogeneity (Szwagrzyk and Czerwczak 1993, Getzin *et al.* 2008), and stochastic processes such as small-scale (gap-phase) disturbance events (Franklin *et al.* 2002). While there has been a plethora of research to date on these ecological and environmental factors and their potential influence on spatial patterning of trees, it remains unclear whether these studies are cross-comparable (for the purpose of synthetic analysis), thereby impeding global generalisation. Condit *et al*. (2000) is currently the exemplar study for explicitly analysing general trends in the univariate spatial-pattern of trees, based on six large (25–50 ha) tropical forest plots; they found evidence for spatial aggregation in many tree species. However, the generality of this finding, and its applicability to forest plots worldwide, remains unresolved.

Here we present the first research synthesis (Ioannidis *et al.* 2015) of the spatial patterns observed globally in forest plots, and look explicitly at the comparability of reported plot data across studies. We aim to: (i) synthesize and determine the reported patterns in forest plots globally, to determine the frequency of aggregation (or randomness) and uncover any representational, geographical or methodological biases in locations or data-collection methods; (ii) test explicitly whether a lack of standardization in plot design, mode of spatial analysis, or choice of metrics reported impacts the conclusions of pattern-based studies; and (iii) use two widely cited process-linked plant traits (i.e., shade tolerance and dispersal vector) to assess the impact of the confounders in (i) and (ii) on the inference of ecological dynamics from spatial patterns.

Materials and methods

Spatial literature database

For aim (i), we searched Web of Science, Scopus and Google Scholar across all available years using the search query (spatial pattern* OR spatial analysis* OR point pattern* OR point pattern analysis* OR spatial distribution* OR spatial processes* OR spatial association*) AND (forest* OR tree* OR woodland* OR stand structure*). From the thousands of initial studies uncovered, we retained only those that: i) tested a null model of CSR and reported a second-order point-pattern statistic (Ripley's K or pair correlation function [PCF]) from which we could extract a pattern type; ii) were implemented for the purpose of assessing spatial pattern (i.e., not methodological); iii) examined spatial patterns of living trees and/or groups of species in 'forest ecosystems' (or 'woody trees' but not woody shrubs). Where analyses were presented graphically (including simulation envelopes) or summarized in tables, the prevailing spatial pattern for both community and individual species was obtained and defined categorically as either aggregated/clustered (C), Regular (Re) or random (Ra). This categorisation depended on whether the observed spatial pattern deviated from the expected null model of CSR and thus, fell above (C), below (Re) or within (Ra) the simulation envelopes, respectively (Wiegand and Moloney 2013). In cases where observations fell both above and below the simulation envelopes at different length scales, the pattern type was reported as both C and Re. These patterns are, however, rare (8.3% communities and 5.4% species occurrences), as were regular patterns (5.9% of species occurrences). Therefore, because of the small sample size for studies that reported Re or C&Re, we focused our analysis for aims (i) and (ii) only on the contrast between aggregated patterns and randomness. An alternative analysis

grouping aggregated and regular as a (non-random) "pattern" and contrasting this with randomness is provided in the Supplementary material Appendix 1; results were similar to the analysis with C and Ra alone. For those studies with multiple sampling dates, only the most recently reported data (community measurements) and spatial patterns were used, to avoid pseudo-replication of forest plots. We also crosschecked the literature to account for circumstances where different studies examined the same plots/forest communities; in these cases, each additional study was given the same ID number and assigned a letter. Taxa that were represented multiple times across different studies/communities (forest plots) were included within the data frame; however, subsampling approaches were applied in the statistical analysis in order to avoid pseudo-replication of species (described in detail below).

Community-level analyses

To address aim (ii), we extracted pattern information for 144 communities and 1022 species occurrences (from 198 communities). North America and Europe were the best represented, accounting for 36.8% and 31.3% of the 144 forest communities, respectively. (Table 1; Fig. 1). We used generalized linear models (GLM) to examine the structural fit of elevation and climatic factors (temperature, precipitation, evapotranspiration) to the proportion of each pattern type (aggregated and randomness). Soil type was not included in our analyses because sample size was not sufficient to compare across all communities.

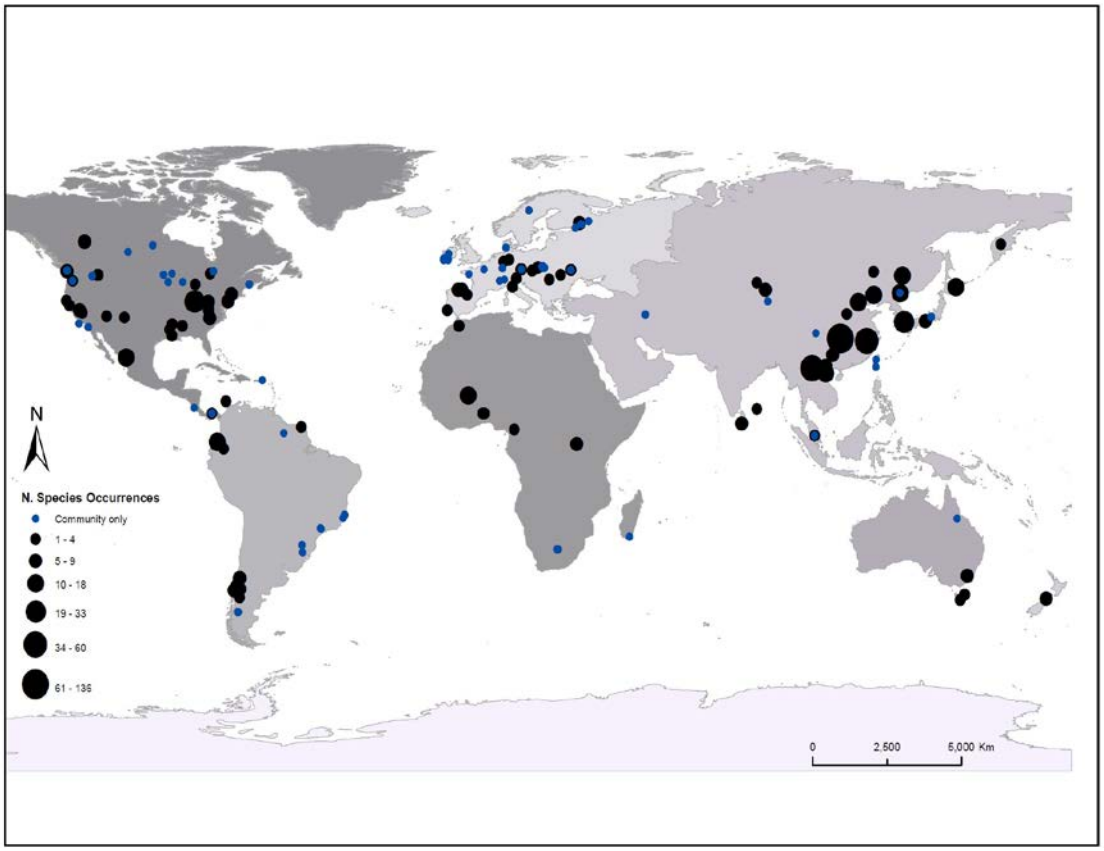


Figure 1: Global distribution of the 198 communities with spatial pattern information for individual species within forest plots (black; many points are overlain) and the 144 plots for which only community pattern information was available (blue). Size of black circles reflects the number of species occurrences per community.

Table 1: Summary of the studies included in the research synthesis, by continent, reporting spatial patterns in forest plots. Key diagnostic variables were, total forested area (FAO Global Forest Resources Assessment; http://www.fao.org/forestry/fra), number of communities represented, number of communities with species pattern information, number of unique species, and number of species occurrences for which pattern information was available. The average plot size and most common tree size measured (minimum diameter at breast height), is also shown.

	Africa	**Asia**	**Australasia**	**Europe**	**North America**	**South America**
Forested area (000 ha)	674,419	592,512	191,384	1,005,001	678,961	883,850
Plots for which we have species pattern reported	16	31	19	58	57	19
Plots we should expect per area of forested land	33	29	10	50	34	44
Species occurrences for which pattern was analysed and reported	40	450	66	146	247	73
Average number of species pattern reported per plot	3	15	3	3	4	4
Average plot size (ha)	4	16	0.4	1	2	8
Tree size measured	>6 cm	>1 cm	All	All & 10 cm	>1 cm & >10 cm	>5 cm

Accounting for plot representation, geographic bias, and methodology

Although we considered the raw information in the subsequent modelling, for our main analyses we constructed two derived datasets; i) geographically corrected, and ii) a geographically and methodologically corrected dataset (Fig. 2). These datasets were prepared *a priori*, because the global distribution of species occurrences was uneven, with Asia being by far the most represented continent accounting for 44.0% of the 1022 species-level analyses, followed by North America with 24.2% (Table 1; Fig. 1); by contrast, there were few species occurrences in Australasia or Africa. When determining the number of communities/plots expected given the area of forested land on each continent and the number of communities for which pattern information has been reported, both Africa and South America are underrepresented (Table 1). We identified two important methodological decisions made by researchers – size (area in hectares, ha) of the monitored plot, and the minimum size (diameter at breast height, DBH) of trees selected for measurement. Plots in Asia were consistently larger than those on other continents, all species patterns in the plots were reported and smaller trees were typically included in the measurements (Table 1). To address all aims, we undertook analyses on the dataset that contained pattern information for individual species occurrences (i.e., data on species identity, dispersal vector, shade tolerance as well as methodological information; plot size, tree size measured, etc.).

The number of species patterns reported per site ranged from 1 to 136, across the 198 communities. Using all species from a single site in spatial analyses might bias the overall pattern type towards the larger and more speciose plots when compared with plots that report and analyse only a subset of the species in the forest community.

These larger plots are almost exclusively in tropical areas (mostly Asia). We tested for the influence of plot representation with two separate analyses (further details in Fig. 2). In both cases, we first bootstrapped (with replacement) the vector of 198 plot identities, and repeated this 10,000 times to obtain summary statistics from a robust sample. In the first case, we selected a single (random) species to represent each plot in a given sample. In the second case, all species from every bootstrap-selected plot were chosen, but then a random selection of 198 species rows were used to create the final sampled data frame. This approach could result in multiple species taken from some plots and none from others, but repeated resampling avoided stochastic idiosyncrasies. The subsequent geographic and methodological corrections (described below) were applied to on each of the one-species and multiple-species per plot sampling protocols.

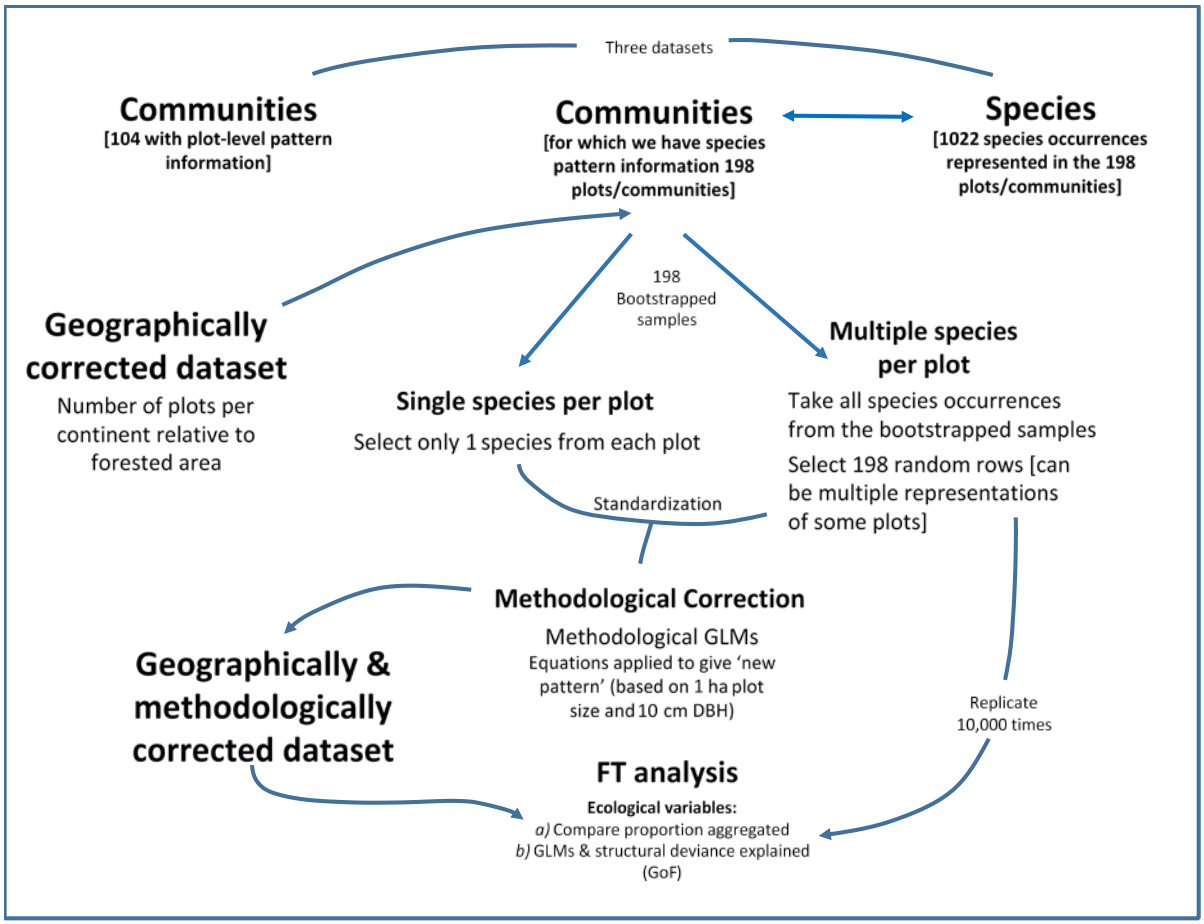


Figure 2: Framework for how the two datasets used in this global synthesis were curated and analysed. The original data is the raw dataset, which was re-sampled randomly (with replacement) to in a way that removed the by-continent geographic bias and plot representativeness (i.e., single or multiple species per community). Generalized Linear Models (GLMs) were used to estimate the ability of methodological choices (plot size, ha and minimum tree size measured, DBH) to explain the proportion of pattern type with the raw and geographically corrected datasets. The statistically best-supported models were applied to provide new, corrected (standardized) datasets; i) geographically corrected and ii) geographically and methodologically corrected based on the probability of randomness observed. Ecological predictors of spatial pattern were then assessed for each of the four data sets.

We tested for geographic bias by: i) calculating the expected proportion of plots per continent, if they had been distributed according to continental forest area, and ii) repeatedly resampling (with replacement) the species-by-community data-set selecting a random bootstrapped selection of 198 rows (i.e., dimensions equal to the original number of communities with species information; Table 1), with the number of samples per continent being set equal to the expected proportions calculated in step i), repeated 10,000 times.

We were also interested in how *a priori* methodological choices might influence the spatial pattern observed in a plot. We tested this by first using a GLM to estimate the relationship between plot area (continuous), and minimum measured tree size (categorical, >1–2.5 cm [small] or >10–30 cm [large] DBH), and their interaction term, when regressed against pattern type (binomial: clustered or random). This fitted model was used to estimate the probability of no spatial structure (i.e., randomness) being *observed* for each individual species occurrence, given the plot size and smallest tree-size measured for that study. The *expected* probability was calculated for a 'standardized' plot of 1 ha area with all trees >1 cm DBH being measured. As a final step, if a random uniform deviate (U ~ [0,1]) was greater than the absolute difference in these observed and expected probabilities, then pattern type was left unchanged. Otherwise, random was switched to aggregated, or *vice versa*. This procedure was repeated for 10,000 resampled datasets, with inference made on the statistics of the bootstrapped data frames.

Using ecological predictors to examine geographic and methodological effects

To address aim (iii) we used binomial GLMs to test a selection of ecological (shade tolerance and mode of dispersal) and climatic/biome correlates, with best-supported models selected using AIC_c. This analysis was completed for the raw, geographically corrected, and geographically plus methodologically corrected datasets (Fig. 2). The proportion of plots that were aggregated, and a measure of the structural goodness-of-fit of the statistical models (percent of deviance explained) were used to compare the two re-sampled data sets (Fig. 2), to explore the effect of geographic bias and methodological choice on the reported pattern type in forests.

Results

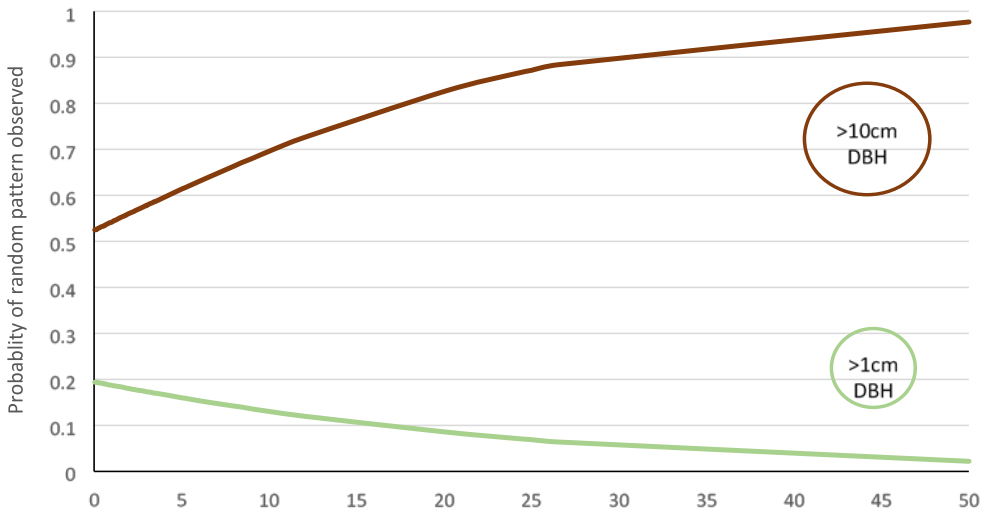
Community-level predictors

Aggregation was the most prevalent pattern type observed for those studies of forest communities that reported second-order point-pattern summary statistics (60%), followed by randomness (18%). Relatively few studies reported regular or multiple [C, Re] pattern types (15%, and 8% of communities, respectively). Of the environmental variables, neither elevation nor climatic factors (saturated model: mean annual temperature, mean annual precipitation and actual evapotranspiration) explained much of the variance in the community spatial patterns (2% and 3% of the structural deviance explained, respectively), with AET as the best-supported model (w = 0.3), explaining 6% deviance.

Species occurrence data: Evidence of methodological choice effect

Of the four possible GLMs that were applied to the geographically unbiased species-occurrence data (null, plot size, tree size measured and the interaction of plot size and tree size measured), the interactive model of plot size and size of tree measured was consistently best supported ($w_{(\text{tree size measured}\times\text{plot size})} \approx 1$). As plot size increased, the direction of the effect varied depending on whether studies included both small and large trees in their pattern analyses, compared to only large trees. The probability of randomness was higher when only the larger trees were measured, and increased continuously with plot size (Fig. 3a). A similar effect of minimum-tree-size measured and plot size were observed for GLMs on the raw data set, but no interaction term was necessary in this case ($w_{(\text{additive})} = 0.73$); this model explained 12% of the structural deviance.

a)



b)

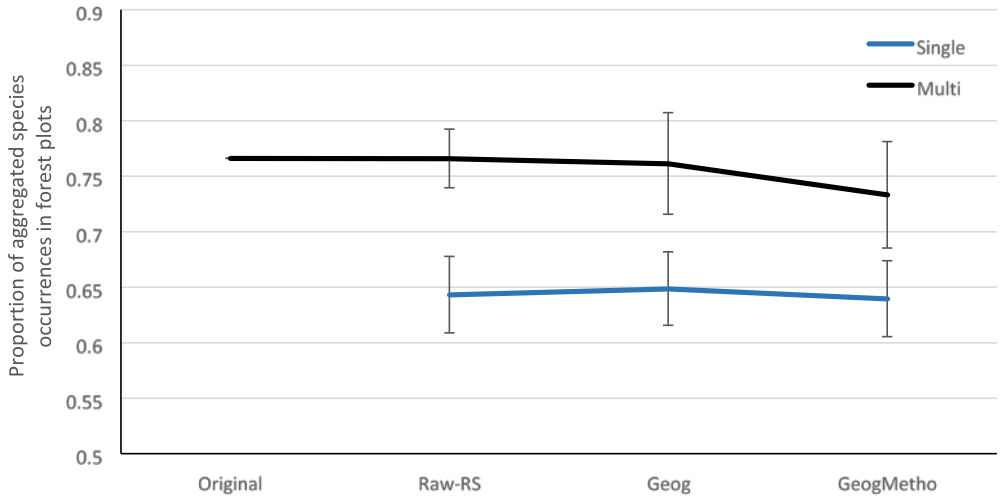


Figure 3: Influence of plot-location (geography) and methodological choice (of plot size and size of tree measured) on the proportion of aggregation observed in forest plots with reported point-pattern results. Panel a) classifies the effect of methodological choice on the probability of observing no spatial pattern (i.e., randomness) in forest plots as plot size (hectares) increases, for both large only (>10, >15, >30) and small minimum tree size measured (>1, >1.3, >1.5, >2, >2.5 cm diameter at breast height) using the uncorrected data. Error bars represent the standard

error (SEM), derived from bootstrapping, and b) shows the effect of data correction on the proportion of aggregation when sampling using a single species per plot, compared to sampling of species occurrences (species may be represented more than once).

Influence of geographic bias and methodological choice on aggregation

Irrespective of the corrections applied to the raw data, aggregation was the most common pattern reported for all species occurrences and across all levels of ecological predictors (Fig. 3b). Overall, 74 – 79% of species occurrences were aggregated (based on sampling multiple species per plot), although after applying the geographic and methodological corrections, this proportion decreased to 68 – 77% (Fig. 3b). Indeed, when not correcting for plot representation, methodological choices or geographic bias the proportion of aggregated species was potentially overestimated by as much as 15% across all factors (Fig. 3b). Conversely, when considering only a single species to represent each forest plot (in any one bootstrap sample), the proportion of aggregation for the raw (sampled) dataset was reduced by 12%, to 64%, and changed little after geographic and methodological corrections were applied. Thus, more speciose plots—if all species are analysed using point-pattern statistics, and the result reported—will tend to skew the resulting global pattern-type observed (Fig 3b).

There was no discernible explanatory power in the ecological variables when using the raw data set (the null was the AIC_c best-supported model in this case) (Table 2a). However, after the plot representation and sampling corrections were applied, dispersal vector was more statistically supported than the null model, based on AIC_c weights (and explained 5.8% deviance, Table 2b). This shows that for an ecological

effect to be detected, the data must be adjusted to sample only a single representative species per plot, and ideally corrected for geographic biases and methodological choice (Fig. 4). Analysis of the fully-corrected data revealed that animal-dispersed species are less aggregated than those dispersed by wind (Fig. 4); this matches synthetic analyses of seed rain (Clark *et al.* 2005). Conversely, there was a tendency for higher proportions of aggregation for shade intolerant species (i.e., 2% deviance explained, Table 2a), but this effect was weak (marginally less supported than the null model, Table 2b).

Table 2: Functional traits as predictors of the aggregation or randomness of trees in forest plots worldwide. Model selection statistics are based on comparing four generalised linear models (GLM), which fitted some combination of shade tolerance (yes/no) and dispersal vector (animal, wind or gravity) to spatial pattern (binomial dependent variable: aggregated or not, based on spatial point-pattern analysis). Shown are the averaged statistics taken across 10,000 bootstrap samples, for a) the original data, and b) after applying sampling corrections (Fig 2). Show are number of parameters (*k*), negative log likelihood (-LogL), corrected Akaike weights (*w*) scaled relative to a total sum of 1, and percent deviance explained (%DE) as a measure of structural goodness-of-fit. For both *w* and %DE, the mean (with 95% percentiles) are shown, to illustrate the distribution of GLM fits across bootstrap samples.

a)

Model	*k*	-LogL	*w*AIC$_c$	%DE
Null	1	-50.53	0.413 (0.022-0.667)	0
ST	2	-49.86	0.277 (0.030-0.709)	1.4 (0.0-7.2)
DV	3	-48.99	0.188 (0.020-0.614)	3.1 (0.9-10.9)
ST+DV	4	-48.33	0.122 (0.018-0.454)	4.5 (0.4-13.7)

b)

Model	*k*	-LogL	*w*AIC$_c$	%DE
DV	3	-53.51	0.310 (0.023-0.724)	5.8 (0.6-15.7)
Null	1	-56.82	0.267 (0.001-0.650)	0
ST	2	-55.69	0.242 (0.003-0.744)	2.0 (0.0-8.4)
ST+DV	4	-52.89	0.181 (0.024-0.545)	7.0 (1.0-17.4)

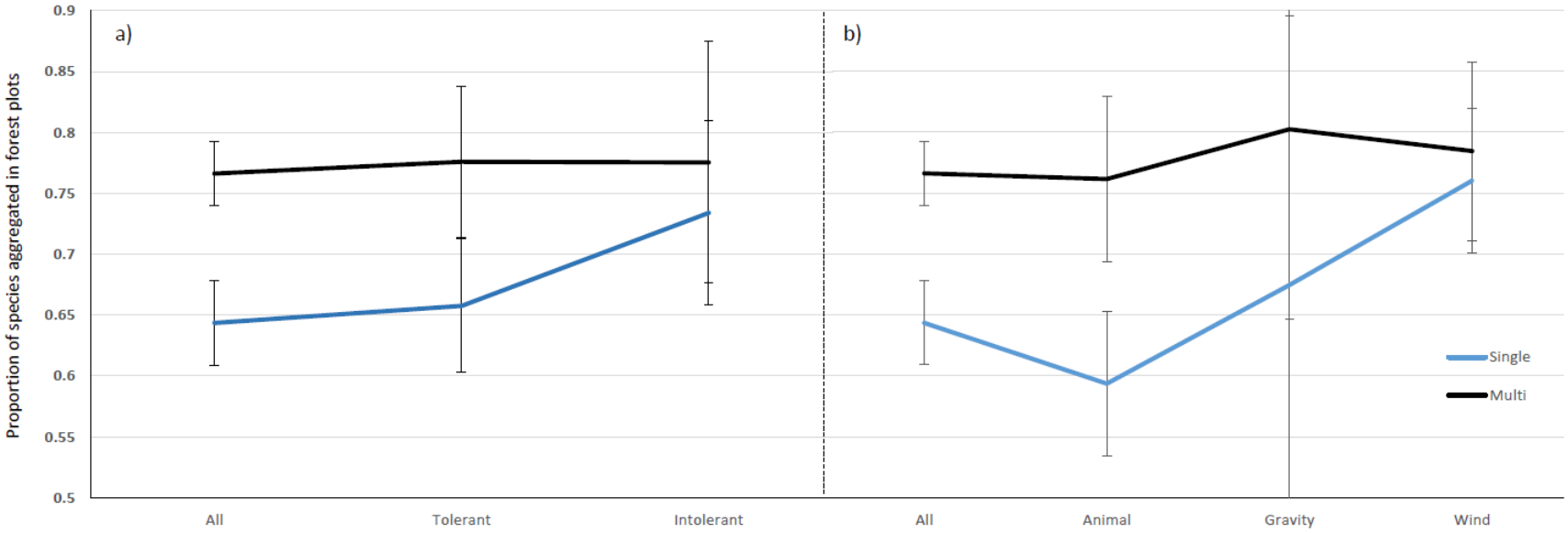


Figure 4: Differences in proportion of aggregation observed for species occurrences within global forest plots, for each level of ecological factor; panel a) shade tolerance (tolerant or intolerant) and panel b) dispersal vector (animal, gravity, wind). The coloured lines show the difference between the sampling techniques; single representative species (blue line) compared to multiple species occurrences (black line - i.e., not controlling for species identity). These results are presented using the geographically and methodologically corrected data frame. Error bars represent the standard error (SEM), derived from bootstrapping.

Discussion

Uniting pattern and process remains a central goal of spatial ecology (Levin 1992, Murrell *et al.* 2001; Murrell 2009). Recent increases in computational power and sophistication of statistical methods has led to a revolution in our capacity to model the patterns embedded in static spatial data, but a suite of complex (often stochastic and historically invisible) processes continue to confound our ability to use pattern information to infer process (Velázquez *et al.* 2016). Many ecological processes with strong spatial components, such as seed dispersal, facilitation and competition, can result in identifiable spatial patterns that conserve an imprint of past processes (Seidler and Plotkin 2006). However, similar patterns might also arise from quite different generating mechanisms, even within populations of the same species (Perry *et al.* 2013). The quest for a link between a 'snap-shot' of pattern and temporally dynamic ecological processes has driven the proliferation of forest mapping studies. In addressing aim (i), we have shown that, among these studies, there is a strong geographical bias in the location of plots reporting spatial patterns, as well as the potential to overestimate the prevalence of aggregation due to *ad hoc* methodological decisions made by researchers. Our systematic review of spatial patterns in global forest plots has also revealed how few published papers have reported results that can be standardized in a way useful for some form of meta-analysis (87 from a pool of thousands of possible forest-pattern-related studies). This lack points to the need for improvements in reporting and consistent study design as crucial steps for the field of spatial ecology, in the quest to link pattern to process.

Influence of biases in plot location and study design

As hypothesised in aim (ii), methodological choices, when integrated globally, can affect the identification and generalisation of global trends in pattern type. The choice of plot size by researchers is driven in part by a need for sufficient sample sizes of trees (i.e., highly species rich communities with abundant stems [of all sizes] tend to not require large plots). These issues of methodological choice are problematic for research synthesises, because the areal extent over which a spatial analysis can be done, and the sample size of measured units, are tied inextricably to plot size and sampling intensity (Dale and Fortin 2014). Because a large proportion of global forest plots are smaller than one hectare, scale-dependent limitations will influence our ability to characterize pattern consistently, and therefore identify common processes (O'Neill *et al.* 1999; Dungan *et al.* 2002).

In this context, it is useful to think of a hierarchy of overlapping but scale-dependent forest processes. Fine-scale effects, in particular, tend to have a strong stochastic element that defies generalization. A mismatch between the characterisation of pattern (e.g. plot size or size of tree measured) and the operating scale of the underlying processes might therefore be common (but difficult to identify for a given study). Indeed, it was only through a synthesis of the global literature of many individual studies that this problem became apparent. Choosing measurement scales that best reflect the process or ecological question of interest could mitigate such issues – yet this is rarely done, both due to the sheer effort involved in setting up plots, and also because we often do not know which scales are important *a priori* (Wiens 1989; Hui *et al.* 2010). In an analogous way, our failure to explain community patterns using global climatic data could be due to these data being too coarse to capture local-scale

effects that interact with the stochastic drivers arising from the dominance of fine-scale influences (e.g., microclimate, topography) at the plot level.

Impact of methodological inconsistencies for linking pattern to process

For aim (iii), we tested two ecological traits (dispersal and shade-tolerance) that have been linked consistently to species-level spatial pattern, but we did not detect a strong influence on reported patterns. Reasons for this lack of explanatory power might include: uneven spread of trait variation across scales, overly coarse classification of spatial pattern, ontogenetic changes in trait expression, and unreported contextual information (e.g., site-specific attributes) that act to mask weaker ecological influences. Ontogenetic variability is possibly the most ecologically interesting, but least considered confounder when attempting to link broad ecological traits to observed patterns (Valladares and Niinemets 2008). For instance, if seedlings of a given species are shade-tolerant, but saplings or adults require exposure to direct sun, then the directionality of effects may cancel out. Furthermore, scale-dependent spatial heterogeneity across larger study areas might favour different axes of a trait, again acting to mask any signal when the entire plot is analysed for patterns. Evidence that microhabitat associations might shift between young (small) and old (large) trees further supports this argument (Comita *et al.* 2007).

A lack of non-randomness in some forest-plot studies does not indicate a lack of process, but instead an interaction, or time-dependence, of a variety of disparate factors, that together result in an apparently ‘random’ outcome. For instance, after a large disturbance event such as a fire or tree-fall, colonization of a gap might be nearly random, with chance groupings of seedlings later amplified by ecological and physical

processes (e.g., suitable soil chemistry, topography, facilitation) or reduced by interspecific competition. Such synergistic and antagonistic forces, acting collectively, might lead to a spectrum of patterns (or apparent randomness), depending on the relative strengths of the contributing processes (McIntire and Fajardo 2009). It is also likely that the datasets that we analysed, consisting of an overwhelming number of small-sized plots, compromised our ability to draw the effect of process out of the categorisation of pattern. This limitation could be overcome if future studies consistently report the raw metrics of spatial patterns (rather than simply testing conformity to a null model with limited information on scale dependency; Velázquez *et al.* 2016), and by use of methods that link spatial-pattern analysis with stochastic, spatially explicit individual-based models (Grimm *et al.* 2005; May *et al.* 2015; May *et al.* 2016).

The prevalence of aggregation observed when using multiple versus only a single species per plot seems to be explicable largely in terms of plot location and methodological choices. Plots where multiple (or all) tree species patterns and all stem sizes were reported tended to be concentrated in a few highly diverse, tropical-climate regions (Fig. 1); these plots were also typically larger in area (often >10 ha) compared to those for which only single or a few species or community-level patterns were reported (common in boreal or temperate zones). Unless only single species per plot is used in a given analysis (ideally, done via repeated subsampling), then this will lead global compilations like ours to amplify the effects of some plots and diminish the signal from less speciose or intensively studied plots. Aggregation seems to be common in tropical forest plots (Condit *et al.* 2000; Wiegand *et al.* 2007), but it remains difficult to differentiate whether this is mainly due to underlying ecological

differences, or because methodological choices (including the lack of representation of tropical species in Africa and South America, given their immense species count) make it difficult to confidently attribute differences in patterns across biomes solely to ecological drivers.

A notable feature of the forest-plot literature is ambiguity regarding whether the study design was testing *a priori* hypotheses about tree patterns, or if the data were analysed *post hoc*. This decision is important because of the potential link between detection of spatial pattern and idiosyncrasies in study design (e.g., choice of plot location, size or species measured or other uncontrolled factors) (Gnonlonfoun *et al.* 2015). When we accounted for geographic bias and methodological choices regarding plot design, we were able to explain more variation in pattern type based on ecological traits. This outcome emphasizes the potential value of having a standard protocol that minimizes non-ecological influences on pattern detection (the CTFS plots published in Anderson-Teixeira *et al.* 2015) is a recent example of the move towards this). Few studies have addressed the influence of plot size or size of tree measured explicitly (Gnonlonfoun *et al.* 2015) and the choice for any individual study is most often pragmatic. Another line of evidence for this effect comes from studies that reported measuring 'all stems'. In these cases, propensity to aggregate more closely resembled that observed for plots where only large trees were included, suggesting that researchers attempted to measure all stems when densities were low enough to make this a feasible proposition. Our observation that large trees exhibit a more random spatial structure fits with the well-grounded theory of competition for space and resources, whereby 'self-thinning' acts to reduce stem density and so leave the remaining individuals less clustered (Li *et al.* 2009; Getzin *et al.* 2011). It is likely that large forest plots (25–50 ha), like those of

the CTFS network (Anderson-Teixeira *et al.* 2015), are best positioned to account simultaneously for joint effects of tree size, ecological determinants, and habitat heterogeneity (Shen *et al.* 2013), yet there are regrettably few of these in today's global forest-plot network (Fig 1), and to date, published studies of reported pattern in the CTFS network are restricted to only a few of these plots.

Directions for future research

One way in which our top-down global synthesis of forest plot data could be improved is by incorporating more comprehensive and standardized site-specific information, such as abundance of individual species along with key geophysical and ecological factors (e.g., soil fertility, topography, local disturbance events, microclimate, etc.) (Ledo 2015). Furthermore, we urge future studies to examine more closely the ecological processes that underpin the general trend of aggregation seen across global forest plots, and just as importantly for contrast, the situations where randomness or regularity are apparent. The studies that seek these generalities should aim to characterize pattern quantitatively, and restrict future synthetic analysis to those studies that are methodologically comparable and geographically unbiased. One such approach may be to analyse the patterns of a consistent number of species using the CTFS standardized network (Anderson-Teixeira *et al.* 2015).

Another potential route to understanding and consolidating global pattern trends in forests is to test a suite of pattern-process models against multiple data sets spanning a range of scales, and including a mix of aspatial and spatial patterns; any one test might be weak or of insufficient coverage, but can be powerful in combination, and help identify predictive failures and highlight structural inadequacies (Grimm and

Railsback 2012). We regard this bottom-up and hierarchical approach as a profitable future direction for forest-plot studies, because it forces an explicit consideration of process, prior to pattern identification. This, in turn, permits cross-validation between individual studies sites, leading to stronger tests of a model's generality.

CHAPTER III

DRIVERS OF SPATIAL PATTERN, DENSITY AND BASAL AREA IN AUSTRALIAN TALL EUCALYPT FORESTS

Forest are complex ecosystems, with their structure and composition determined by multiple, often interacting, processes. Here we focus on two key drivers of forest structure—climate and disturbance—using a recently established network of 48 × 1-hectare censused plots spanning the Australian tall eucalypt forest estate. Using spatial point pattern analysis, we find that aggregation is the dominant spatial pattern at both the community- and species-level. Eucalypts showed clumped patterns across 62% of the plots and dominated the total basal area (83% average within the plot). The mid- to understory non-eucalypts were also mostly aggregated (in 85% of plots), but these dominated total tree density (85%, with many smaller stems) rather than basal area. We used generalized linear modelling to determine the predictors of this spatial patterning, as well as plot-level density and basal area (surrogates of long-term productivity). Biotic variables best explained community spatial patterns (15% of cross-plot deviance explained), whereas abiotic factors were most important for the

dominant-species patterns (21.3%). Climate was a strong predictor of non-eucalypt basal area and density, and eucalypt basal area (but not density), consistently explaining >40% of the deviance in these variables. This study demonstrates the importance of climate and disturbance in driving the structure of the tall eucalypt forests of Australia.

Introduction

Spatial and abundance patterns are imprinted with the processes that have shaped forest structure and dynamics through time, which analysis of the statistics of point locations can reveal. As a consequence, spatial point-pattern analysis has become a standard tool for ecological studies of coordinate data of trees in forest communities worldwide (Velázquez *et al.* 2016). For example, aggregated (clumped) patterns in a forest community might indicate that a group of species has regenerated in a canopy-gap following a disturbance event. Over time, competition between immediate neighbours will ensue, with density-dependent mortality thinning out the clumps, potentially leading to the formation of regular spatial patterns as canopy trees reach maturity (Moeur 1997; Getzin *et al.* 2008). In addition to plant-plant interactions, spatial patterning can be driven by environmental heterogeneity, both within sites (e.g., clustering along waterlines, specific soil types, or due to local topographic variation) and across sites (e.g., due to climatic influences) (Fangliang *et al.* 1997). Such relationships are of interest, because ecologists are still constrained in their ability to predict spatial structures manifest in the same forest type over broad geographic and climatic ranges.

Beyond the spatial distribution of individual trees, the long-term productivity of forest ecosystems (as measured by standing patterns of biomass and structure, such as density or basal area) will also be shaped by top-down climatic conditions (e.g., available energy, precipitation or seasonal extremes), biogeographic factors (e.g., historical refugia, nutrient content of soils), and functional traits of species (e.g., shade tolerance or dispersal vector) (Paquette and Messier 2011; Reich *et al.* 2014). However, it is difficult to generalise across studies of different forests, due both to uncontrolled variation such as methodological choice (such as plot size or field methods) and forest type, along with limits on the coverage of samples that span wide continental scales. To date, studies linking spatial patterns and structure to inferred processes include forests of the Afrotropics (e.g., Friis 1992), boreal forests of Minnesota (Frelich and Reich 1995), and *Picea-Fagus* forests of East-Central Europe (Szwagrzyk and Czerwczak 1993), with most research concentrated in tropical regions (due in part to the establishment of multiple large 25–52 ha plots in tropical countries (Condit *et al.* 2000; Wang *et al.* 2010; Wang *et al.* 2011; Anderson-Teixeira *et al.* 2015).

Australia, however, is relatively under-represented: the few studies examining the underlying spatial pattern and standing structural patterns in forested areas include the species-rich shrublands of Western Australia (Perry *et al.* 2008; Perry *et al.* 2013; Perry *et al.* 2017), savanna vegetation in the Northern Territory (Pearson 2002), stands of Huon pine *Lagorostrobus franklinii* (Gibson and Brown 1991) and *Eucalyptus obliqua* monocultures in Tasmania (West, 1984), and tropical rainforest species (Webber *et al.* 2010). Yet, there has been no such surveys across the macro-gradient of tall eucalypt forests in Australia (the most extensive forest biome on the continent),

perhaps because they have been considered broadly equivalent to temperate broadleaf biomes from the northern hemisphere.

Here we test this supposition, by asking: (i) whether Australian tall eucalypt forests exhibit similar spatial and structural patterns to structurally equivalent forests worldwide, and (ii) if these patterns are predictable across the continent, based on climatic or biogeographic factors. This cross-scale analysis has become possible thanks to a new database created from the AusPlots Forest Monitoring network (ausplots.org), consisting of 48, 1-hectare (100 × 100 m square) permanent plots established in the tall eucalypt forest biome between 2012–2015, and spanning the eastern, southern and western coastal regions of Australia (Fig. 1). This network was established as part of the Terrestrial Ecosystems Research Network (TERN), and included measurements of tree height, diameter at breast height (DBH), spatial location of every individual >10cm DBH, species identity and tree status (alive or dead) (see Wood *et al.* (2015) for further details on the establishment and characteristics).

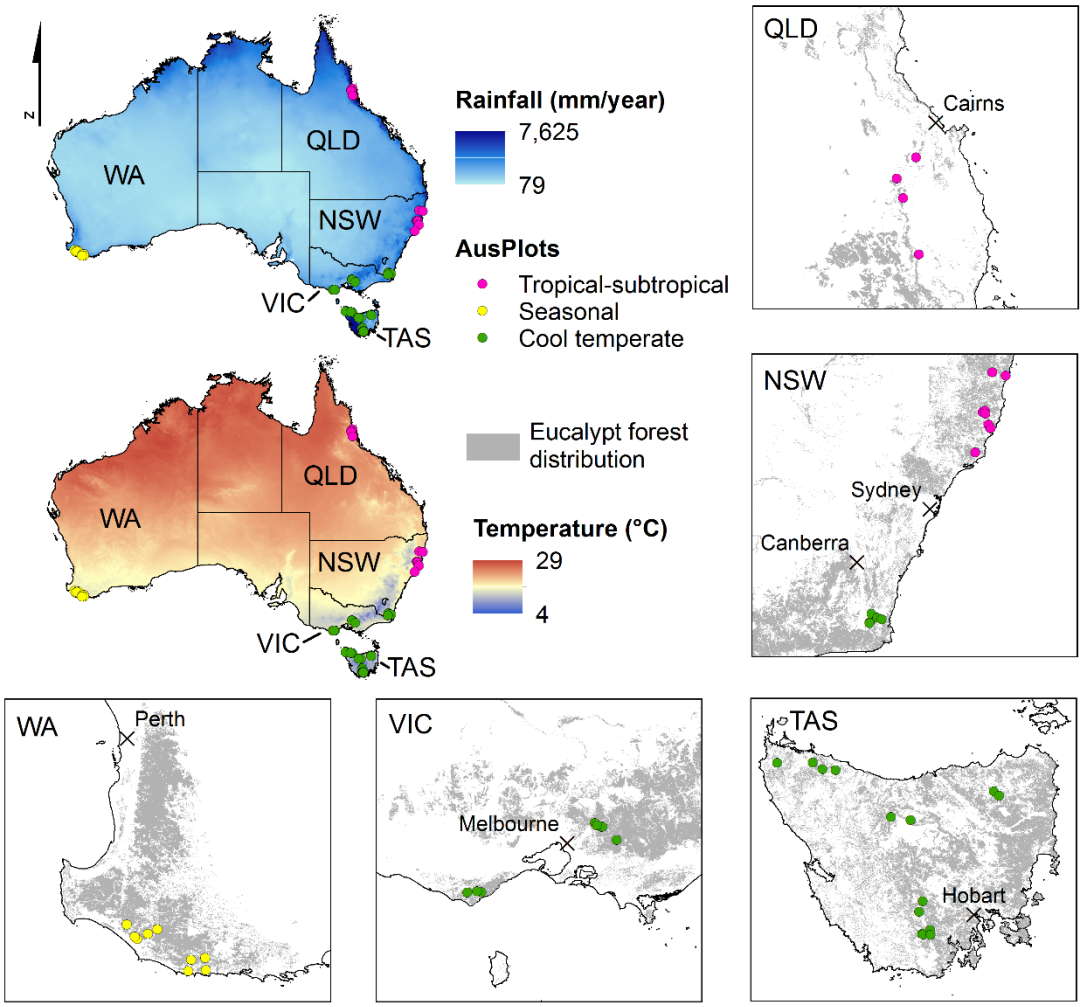


Fig. 1: The distribution and location of the 48 AusPlots forest plots across the broad macro-ecological climatic gradients of Australia. The colour of the dots shows the habitat classification. The grey shading shows the eucalypt forest distribution, the blue and red shading on Australia highlights the mean annual rainfall and temperature, respectively, across the country.

Materials and methods

Spatial point pattern analysis - Univariate

The underlying spatial pattern of communities (pooled over species) and species (> 20 individuals per plot) was determined using spatial point pattern analysis. We used the pair correlation function (PCF) to describe patterns and the linearisation and variance-stabilising correction of the K-function (Ripley's K) L(r) to explore how well alternative point-process models characterise them (following Perry et al. 2008). Strength of departure from the null model of complete spatial randomness (CSR) was determined using the model fit (*u* rank), Clarke and Evans statistic and Donnelly summary statistic, and was aided by visual inspection of the diagnostic plots (see Spatial null models section below and; Wiegand and Moloney 2013). Under CSR, L(r) = 0; aggregate patterns show L(r) > 0 and regular patterns L(r) < 0. The edge corrections described by Goreaud and Pélissier (1999) were used, and we calculated L(r) and g(r) at 0.1m intervals up to a distance of 25m.

Spatial null models

Aggregation can arise from either first order (gradient) or second-order (true-clustering) properties of the pattern (i.e., location of the individuals in the forest community; Perry *et al*. 2008). First-order patterns indicate a lack of interaction between the points (e.g., individual trees) and arises from variation in the density (intensity) of stems across the forest community in response to an underlying environmental gradient (e.g., in soil conditions or topography, in a forest context). Second-order patterns, however, do imply interactions between points (individual trees) that can be a result of biotic (e.g., plant-plant competition) or abiotic (e.g., areas

of high light or nutrient availability) factors. To characterise the observed spatial patterns, and distinguish between the two types of aggregation – first-order and second-order, we generated simulation envelopes using three alternative null models; the Homogeneous Poisson process (HPP), Inhomogeneous Poisson process (IPP) and the Poisson Cluster process (PCP). For further details on the null models and how they distinguish between first- and second- order aggregation, see Perry *et al*. (2008). To assess model fit, simulation envelopes were calculated at alpha = 0.01 based on 499 Monte Carlo simulations. To assess deviation from the various null and alternative models we used the Cramer von Mises (CvM) statistic, which is the sum of the squared deviation of the observed from the expected across all distances (Perry *et al.* 2006); for the HPP, IPP and PCP we used the mean of the Monte Carlo simulations as the expected value (Perry 2006; Perry et al. 2008). The R library spatstat v1.50 (Baddeley and Turner 2005) was used for all spatial analyses using R v3.4.0 (R Core Team, 2017).

Predictors of pattern, density and basal area

We used likelihood-based generalized linear modelling (GLM) to relate three plot-based metrics for forest structure to abiotic and biotic predictors. The dependent variables were tree density, total basal area, and spatial pattern (as determined using the Ripley's *K* statistic). Density and basal area, being continuous and strictly positive, were fit using a Gamma distribution family (log link), in aggregate across all trees, and separately for eucalypts or other trees (with DBH > 10 cm). The spatial pattern was categorised as either aggregated or not (denoted as 1 or 0 respectively) depending on the fit of the best-model and visual examination of the graphic output. Patterns were then fit with the binomial family (logit link), and tested on both the community

(all tree species) and just the dominant canopy eucalypt at a given plot (as defined by basal area, for those with > 30 individuals). The predictor variables tested for density and basal area were strictly climatic (derived from Worldclim 2 at 30 arc-second resolution: worldclim.org): mean annual temperature (MAT), temperature of the driest quarter (MT_DQ), annual temperate range (Trange), mean annual precipitation (MAP), precipitation in the coldest quarter (PCQ) and precipitation in the driest month (PDM). For spatial pattern, we tested: (i) climate predictors (see above); (ii) biotic predictors (average tree size, total basal area, and number of species [corrected for sampling intensity using the multiton method; (Alroy 2017); (iii) a three-level biogeographic (biome) factor (plots categorised into tropical/subtropical, cool-temperate, or seasonal forests); and (iv) for the species-level analysis only, the following functional traits (coded as two-level factors for yes/no): shade tolerance, resprouter, nitrogen fixer, plus dispersal vector (three levels: animal, wind or gravity). The percent deviance explained by the saturated model (all additive terms) was determined, as was the AIC_c top-ranked model (Burnham and Anderson 2003) based on simplified subsets of these *a priori* predictors. All GLMs were fitted and evaluated in Program R v3.4.0 (R Core Team, 2017). All statistical analyses are summarised in Table 1.

Table 1: Summary of the ecological questions and hypotheses explored in this study, and the methods (analyses) used to address them.

Ecological Questions/hypotheses	**Analyses**
Spatial analysis - Univariate *Community (1 ha plots – all stems)* 1. Do plots in the same forest type (tall eucalypt forests) show the same pattern type?	Spatial point pattern analysis, test against departure from complete spatial randomness (CSR).
2. Is the observed aggregation best described by environmental heterogeneity across Australia, or interactions between individual trees?	Evaluate departure from CSR using two alternative models; inhomogeneous Poisson process (first order aggregation) and a Thomas cluster process (second-order aggregation). Assess model fit using Clarke-Evans, and Donnelly statistic, visual examination of graphics and (u + rank).
Species (>30 individuals) 1. What is the most prevalent pattern type for species across Australia in the tall eucalypt forests? a) Across each habitat? b) Between guilds (scl, rf, euc)?	Group by guild (i.e., eucalypt, sclerophyllous or rainforest species) and evaluate pattern-type (departure from CSR). Run a GLM testing the influence of guild as a predictor of species patterns.
2. Is the observed aggregation best described by environmental heterogeneity, or interactions between individual trees of the same species?	Evaluate departure from CSR using two alternative models; inhomogeneous Poisson process (first order aggregation) and a Thomas cluster process (second-order aggregation). Assess model fit using Clarke-Evans, and Donnelly statistic, visual examination of graphics and (u + rank).
Climatic drivers of forest structure 1. Is climate an important predictor of eucalypt and non-eucalypt density and basal area and what are their relationships?	Generalized linear modelling (GLM) approach. All subsets of climate models tested (after checking for correlation). Best climate model for each dependent variable determined using wAICc and deviance explained. Report deviance explained, model fit and effect plot of the best model for each dependent

	variable. a) Linear model of *a priori* combinations of total density and total basal area with eucalypt and non-eucalypt density and basal area.
Predictors of community and species patterns 1. Are spatial patterns best described by biotic (average tree size, total basal area, number of species), abiotic (MAT, Trange, MT_DQ, MAP, PDM, PCQ), or habitat (temperate, seasonal, tropical-subtropical) for: a) Community (all stems) spatial patterns and b) Dominant species patterns	Generalized linear modelling (GLM) Biotic saturated model vs. abiotic saturated model (% deviance explained) compare to biogeographic predictor (habitat). Rank models by *w*AICc. Report deviance explained and fit for best model.

Results

Spatial patterns – communities (all stems)

Aggregation was the most common pattern type across the tall eucalypt forest plots of Australia (62% aggregated, 15% random, and 23% regular). Of the 62% of plots that were aggregated at distances of up to 20 m, there were distinct groupings in the percentage (%) of communities exhibiting aggregation across habitat types (e.g., seasonal and temperate 67%, and tropical-subtropical 42%). Tropical-subtropical habitats showed the highest fraction of regular and random plots (33% and 25% respectively), while temperate and seasonal were consistently lower at 22% and 11%. Half of communities conformed to a homogeneous Poisson (CSR) model, whereas 23% fit best to an IH, and 27% to a CP.

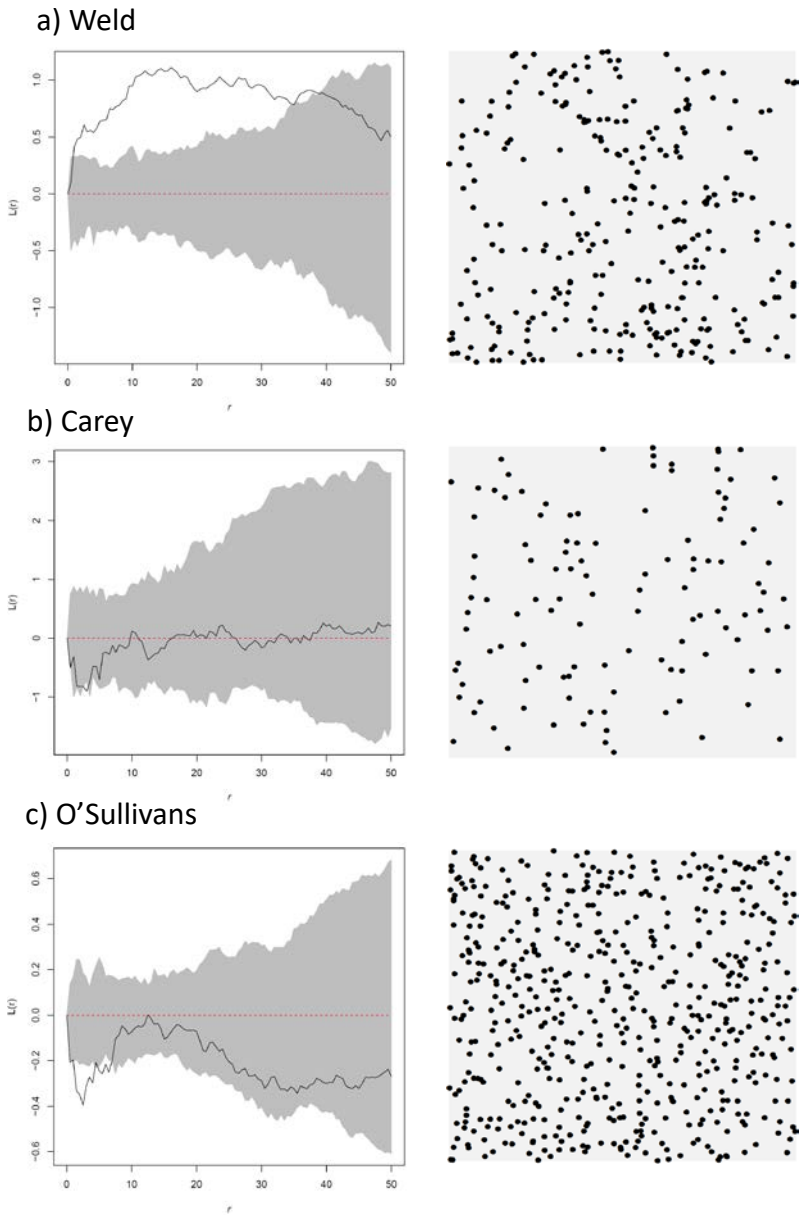


Fig. 2: Example of three different types of community-level patterns (aggregation [a], randomness [b], regular [c]) and their corresponding L(r) functions, confidence envelopes (grey shading), at the $\alpha = 0.01$ level using an inhomogeneous Poisson model. The column of figures on the left show the positions of all stems in the 1 hectare plot.

Spatial patterns – species and species occurrences

There were 153 species occurrences across the 48 × 1-hectare eucalypt-dominated AusPlots, drawn from a pool of 55 unique species of tree >10 cm DBH. The most common pattern for all species occurrences was aggregation (73%), followed by randomness (20%), with few exhibiting regularity (7%). Aggregation was most often observed at shorter distances ($45\%_{0–5m}$ and $25\%_{>5m–20m}$ of total species, respectively), with regular patterns also following this trend ($7\%_{0–5m}$ vs. $4\%_{>5m–20m}$, respectively).

There were consistent species patterns across habitat zones in Australia – tropical-subtropical areas had the highest percentage of aggregated species (77%), followed by cool-temperate (73%) and seasonal (65%). Regularity was rare for all species occurrences, being only detected in seasonal, and cool temperate habitats (11% and 8% respectively). When grouping species occurrences by guild, sclerophyll and rainforest species (non-eucalypts) were indistinguishable in pattern type, with 84% and 82% aggregated respectively, compared to eucalypts of which only 60% were aggregated (see SI results 2a). More non-eucalypts were aggregated than eucalypts across all distances ($Z_{0–20m} = 3.05$, $SE_{0–20m} = 0.43$; SI results 2b).

Predictors of eucalypt and non-eucalypt density and basal area

Climate was a strong predictor of eucalypt basal area, and non-eucalypt density and basal area (Table 2). Cross-plot variation in eucalypt density, however, was less influenced by climate, with ~ 15% lower deviance explained (DE) than the other saturated models. The best predictors for both non-eucalypt density and basal area were MAP, Trange and MAP, MT_DQ for eucalypt density, and the combination of

MT_DQ and PCQ for eucalypt basal area (Table 2). The direction of the effects is crucial for understanding the dynamics of these two groups, as both the slope and direction of their response to these predictors differs (Fig. 3). The basal area and density of eucalypts is higher when MT_DQ is low and PCQ is high. Conversely, greater non-eucalypt density and basal area are associated with high annual rainfall and narrow temperature range (Fig. 3).

Table 2: Summary statistics of the best climatic-based generalized linear models for predicting density and biomass (basal area) of Australian eucalypt forest plots.

	Eucalypt density	Eucalypt Basal area		Non-eucalypt density		Non-eucalypt Basal area	
$Predictor_{best}$ [+]	MT_DQ	MT_DQ	PCQ	MAP	Trange	MAP	Trange
Estimate	-0.07	-0.06	0.001	0.003	-0.18	0.002	-0.25
STD error[*]	0.02	0.01	0.0003	0.0004	0.06	0.0004	0.06
T value	-3.82	-4.60	4.98	6.53	-3.02	5.89	-4.49
% DE_{best} [#]	22.5	31.5		37.7		40.1	
% DE_{sat} [^]	29.3	43.3		41.4		41.1	

Footnotes: [*]Standard error. [#]Deviance explained by the AIC_c best model (as shown in the '$Predictor_{best}$' column). [^]Deviance explained by the saturated model (containing all climatic variables in an additive model).

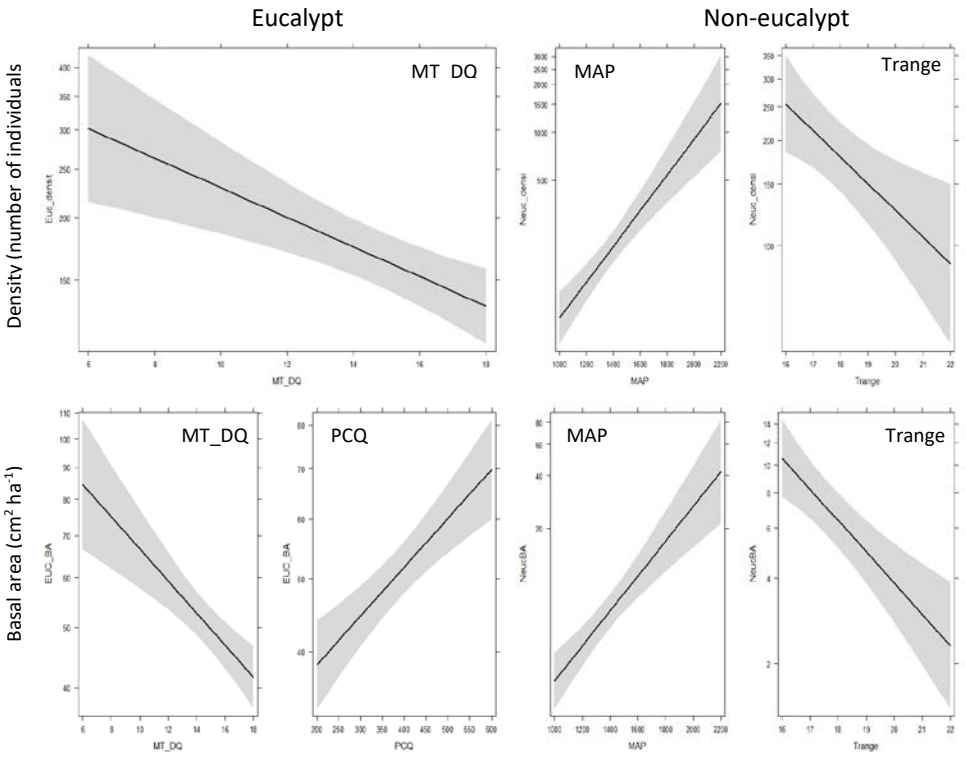


Fig. 3: Relationship between density (number of individuals), basal area (m^2 ha^{-1}) and climatic variables for both guilds (eucalypt and non-eucalypt).

Community density across the 48 plots is driven by the non-eucalypts (because these contain many more individual trees), whereas total basal area is mostly determined by the eucalypts, these being the dominant large canopy trees (Figs. 4 a, b). Non-eucalypt basal area is highest when fewer eucalypts are present, and as eucalypt density increases the contribution of non-eucalypt basal area diminishes (Fig. 4 c). There is no relationship between eucalypt and non-eucalypt basal area (r = 0.014, p = 0.925), nor for density (r = 0.02, p = 0.893). There is, however, a strong positive linear correlation

between density and basal area of non-eucalypts (r = 0.794, p < 0.001), but it is only weak for eucalypts (r = 0.282, p = 0.052).

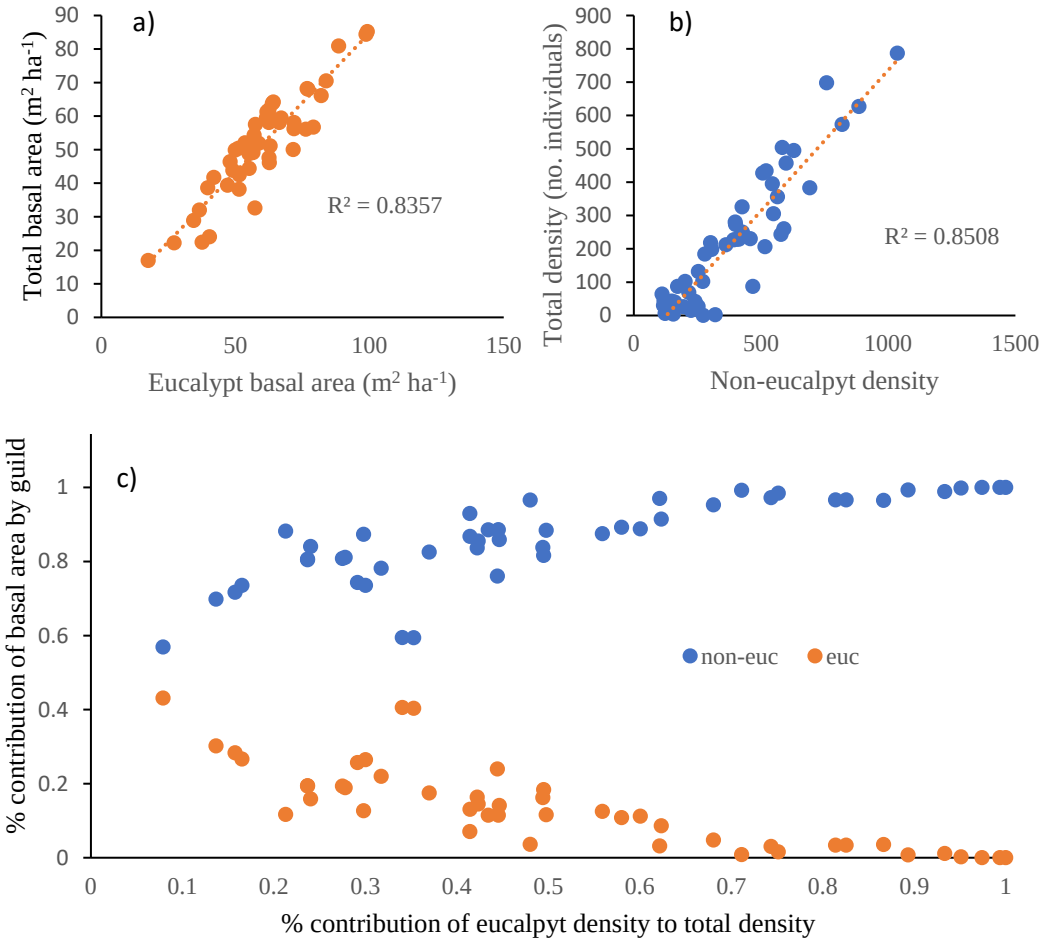


Fig. 4: Drivers of total density and total basal area for the 48 Australian 1ha plots. a) relationship between total basal area and eucalypt basal area, b) relationship between total density and non-eucalypt density and c) relationship between the percentage contribution of basal area by both species and the percentage contribution of eucalypt density to total density.

Predictors of community and species patterns

Communities

Biogeography (biome) was not a useful predictor of community spatial patterns in Australian tall eucalypt forests (%DE = 1.6 for the saturated model). The biotic model explained slightly less variance (%DE = 15.6) in pattern type than the abiotic model (%DE = 16.4). A combination of average tree size and number of species was the most parsimonious simplified model overall ($wAIC_c$ = 0.52, %DE = 15.0), suggesting a tendency towards aggregation with smaller tree sizes and fewer species present in a forest plot. The best abiotic predictor(s) was a single term: temperature range ($wAIC_c$ = 0.119, %DE = 6.5).

Dominant eucalypt patterns

For the dominant eucalypt species, biogeography was again a poor predictor of eucalypt pattern (%DE = 4.8). Abiotic variables explained more variation than biotic when comparing the saturated model sets ($abiotic_{sat}$: %DE = 23.5, $biotic_{sat}$: %DE = 11.6). Overall, the AIC_c best model for dominant-eucalypt spatial pattern was MAT, PCQ, Trange ($wAIC_c$ = 0.248, %DE = 21.3), revealing higher aggregation in areas that were cooler, had lower precipitation during cold quarters of the year, and experienced narrower temperature ranges (Fig. 5). Functional traits were not useful predictors for any individual species pattern (see SI results).

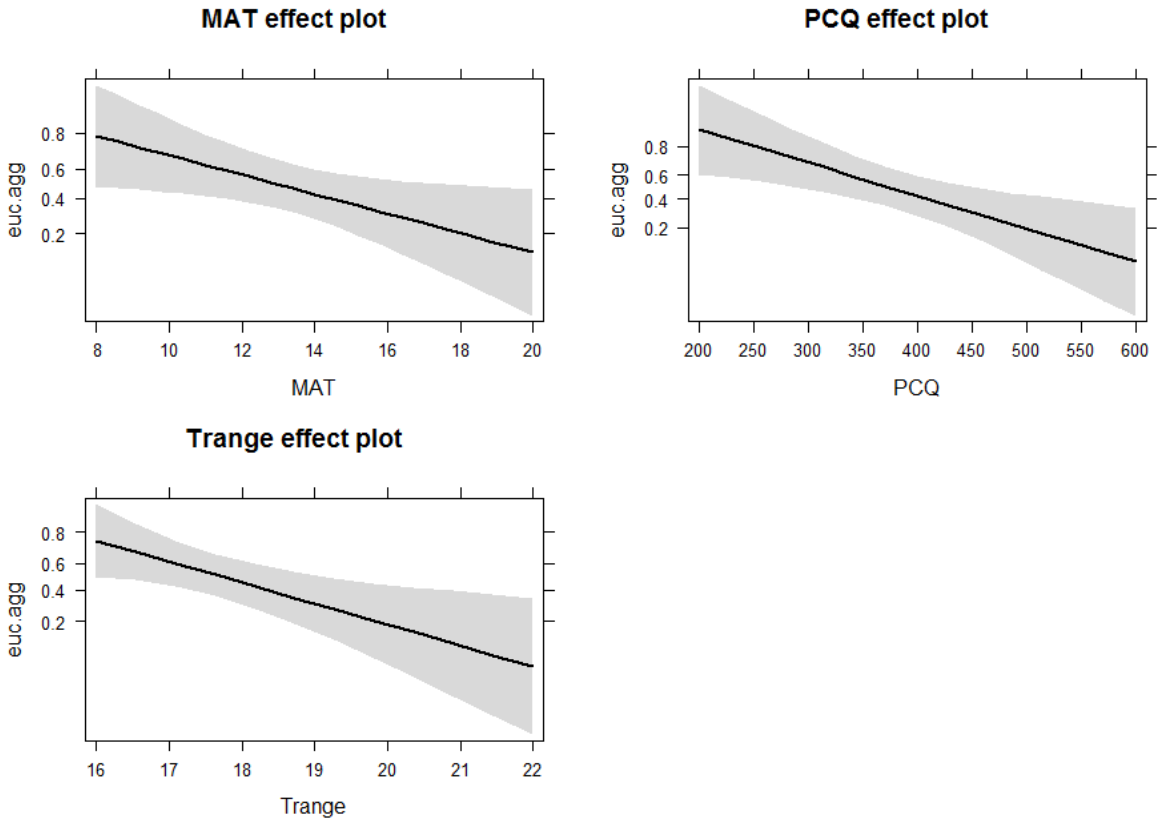


Fig. 5: Effect of climatic variables on the proportion of aggregation species observed for the dominant species (eucalypts) across the 48 × 1 ha plot network.

Discussion

The underlying spatial patterns of the tall eucalypt forest system, as characterised by the new 48 one-hectare AusPlots network, support the global prediction that aggregation is the most common pattern in communities, particularly at local scales (Plotkin *et al.* 2002; Zhang *et al.* 2012). Individual species in the AusPlots also exhibited aggregated patterns (particularly at short distances, 0–5 m, and for the smaller, non-eucalypt species). Traits such as shade-tolerance and dispersal vector have been shown to be highly correlated with pattern-type across multiple ecozones worldwide (Seidler and Plotkin 2006; Wang *et al.* 2010). However, these were not informative on spatial pattern for any individual species in this study, perhaps due to the emergent habit of the dominant eucalypt species (Attiwill 1994), and because structuring of these forests is driven by frequent disturbance and climatic variation, which are not species specific, as distinct from filtering via individual species traits (Bonan 2008).

Climate, particularly water availability and temperature, apparently exerted a strong influence on the structure of both eucalypt and non-eucalypt 'guilds'. Eucalypt density was most sensitive to mean temperature of the driest quarter, and eucalypt basal area coupled this with precipitation in the coldest quarter. Non-eucalypt species were also affected by temperature and precipitation, with both density and basal area responding to changes in mean annual precipitation and temperature range. Although suggestive of an analogue response of the two guilds to climate, the direction of their responses was contrasting: while both guilds were positively affected by enhanced water availability, they showed opposite responses to temperature. While non-eucalypts

thrived with narrower temperature ranges (indicating avoidance of temperature extremes), eucalypt density and basal area were higher in cold-dry conditions. Climatic variables were poor predictors of basal area for eucalypts, perhaps because local adaptations were smeared out across a continental scale. The differences observed here between eucalypts and other species suggest a decoupling of the guilds. But if climate is not a strong predictor of eucalypt density and basal area, what is their main driver?

It is possible that spatial heterogeneity, caused by disturbance, soil chemistry or micro-topography, could be influencing the structure and dynamics of the eucalypt and non-eucalypt components of these tall forests in different ways (Harms *et al.* 2001). Many eucalypt species are favoured by fire (which is often rare but intense in the cool-temperate regions), possessing functional traits such as epicormic resprouting and protection of regenerating buds, which allow them to survive and regenerate after a fire (Ondei *et al.* 2016). Such adaptations confer eucalypts an ecological advantage over other species in locations typified by high fire frequency, particularly over those that are fire-sensitive. This hypothesis is supported by observations in other fire-prone eucalypt-dominated habitats, such as the Australian tropical savannas. There, the highly seasonal rainfall was an important predictor of basal area of both guilds, but with stronger effects on non-eucalypts (Lawes *et al.* 2011). The latter study concluded that fire and rainfall were likely to be the limiting factors preventing an increase in non-eucalypt basal area and thus facilitating eucalypt dominance. In our study, we could not distinguish or analyse these factors separately, but we do hypothesise that there is some apparent decoupling between the drivers of the two components/guilds of the forest.

The Australian tall forests are characterised by giant, long-lived eucalypts that dominate the upper canopy (Attiwill 1994), while non-eucalypt species, found mostly in the mid- and understorey, are more evanescent, due to dynamic processes including density-dependent mortality, fluctuating gap availability and frequent minor disturbances (e.g., treefall, low severity fires, herbivory, and trampling by small macropods; (Gill 1997). It follows that eucalypts constitute most of the woody basal area, and hence drive most of its variation, while non-eucalypt trees are on average smaller but more abundant, and thus have strong influence on community density. If this decoupling is indeed a general rule, then it suggests a need to be cognisant of the differences in responses of the eucalypt and non-eucalypt when designing management and conservation actions; these are likely to be ineffective if applied to the forest as a homogenous whole. Our results from the AusPlots network suggest many interesting directions for follow-up research on Australian tall eucalypt forests, including: (1) examination of local-scale microclimatic factors to test whether this continent-wide signal of decoupling exists at local (e.g., plant-plant interaction) scales, and (2) evaluation of antagonism as a driver of structure: is intra- or inter-specific competition most prevalent within the eucalypts? Such hypothesis-driven empirical research will be crucial for attempts to model how, under Anthropogenic global change, shifts in future climate and disturbance will shape the future structure and composition of Australia's unique tall eucalypt biome.

CHAPTER IV

LATITUDINAL CONTROLS ON FOREST SPECIES RICHNESS ARE NOT DIRECT

With rapid anthropogenic climate change, understanding the drivers of species diversity and productivity in ecosystems is critical for identifying effective solutions for management and protection. Factors influencing community patterns in forests have been studied and debated for decades, focusing largely on latitudinal or localised diversity gradients. Here we analyse an assemblage of global forest-plot data, with controls for sampling intensity, to evaluate relationships between the drivers (latitude, climate, and biome) and responses (species richness, evenness and basal area) of community structure and composition. Our results reinforce the common-sense notion that latitude is a useful 'top-down' predictor of species richness in forests. However, using structural equation modelling we show that this pattern is largely due to its indirect influence on climatic variables (with consequences for energy and water availability), coupled with specific biogeographic controls. The direct climate link to species richness is important, because it implies a strong sensitivity of forest biodiversity to climate change.

Introduction

The general decline of species richness in ecological communities, from equator to poles, and the specific patterns and causes of this latitudinal diversity gradient (LDG), have been debated for almost a century (Pianka 1966; Jablonski *et al.* 2006). This biogeographic problem has been studied in a wide variety of taxa, including birds (Hawkins *et al.* 2003b), plankton (Powell and Glazier 2017), stony corals (Spano *et al.* 2015), ferns (Nagalingum *et al.* 2015) and parasites (Torchin *et al.* 2015). Numerous hypotheses have been proposed to explain the existence of the LDG, but this has led to controversy, because of potential interdependencies, lack of rigorous falsification, and the predominance of single-gradient studies that apparently counteract the notion of generality within the LDG (Willig *et al.* 2003). Furthermore, while recent studies focused on ecological explanations of LDG, such as life-history and functional traits, the specific processes that determine species co-occurrences and community complexity are often under explained or analysed, and over-generalised (Rohde 1999). For example, mid-domain models, which predict a peak in species diversity towards the centre of large land masses (such as equatorial Africa), are often invoked without an eco-evolutionary underpinning, and the array of subsequent tests using these models consistently impose constraints (e.g., on the range size of species), or use latitude as a surrogate variable for another attribute with which it co-varies (Hillebrand 2004). With increasing anthropogenic global change, the resolution of the causes of the LDG never been so crucial. Such theory, for instance, supports decision making by indicating where to direct conservation actions, such as the biodiverse and threatened tropics (Brown 2014).

The link between of species richness, productivity and latitude has also inspired much debate in the ecological literature; both the occurrence of, and explanations on, the mechanisms driving LDG have challenged ecologists for decades (Hawkins *et al.* 2004). Theories have predominately predicted either a unimodal (Qian *et al.* 2009; Fraser *et al.* 2015), or a positive absolute relationship between these variables (Stirling and Wilsey 2001; Tilman *et al.* 2001). Many adopt the premise that understanding the form of the relationship between species richness and productivity will allow the development of general models of ecosystem assembly and maintenance that will guide theory and management at multiple scales (Fraser *et al.* 2015). However, these studies have only considered one component of the relationships between species diversity or productivity and latitude, and said little about the drivers of both.

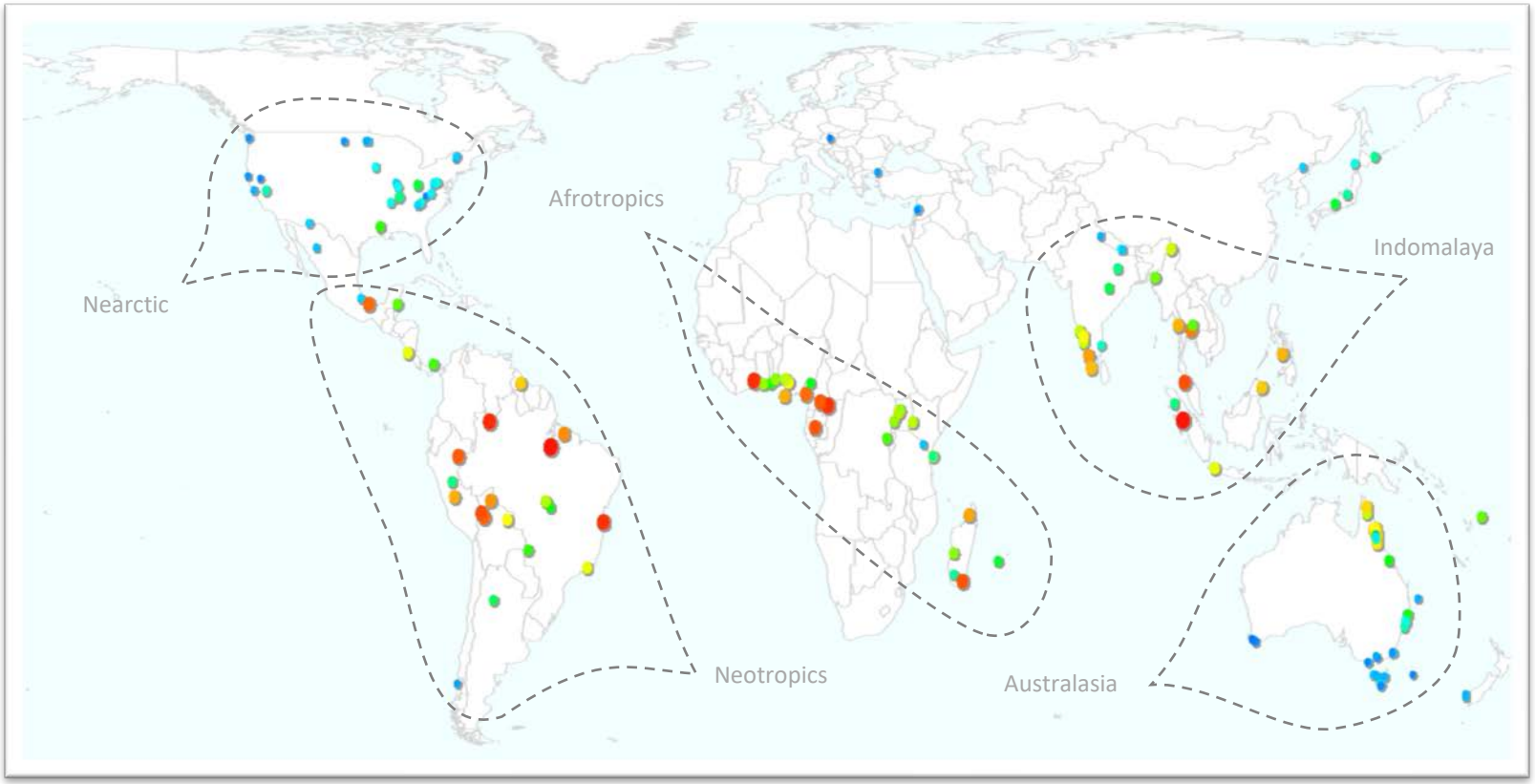
We aimed to test the common assertion that latitude has a direct influence on species diversity, evenness and productivity in worldwide forests. To do this, we use a novel combination of approaches, including: (i) multiton sampling to estimate plot-based species richness (an approach that more effectively accounts for finite observations of rare species), and (ii) path analysis and generalised linear modelling on two comprehensive, standardised datasets: one that covers all major forest biomes worldwide, and another that surveys in depth a single forest type for the entire Australian continent (analysed for the first time). Moving closer towards a resolving this debate is critical if we are to address and mediate threats to biodiversity in the Anthropocene.

Materials and methods

Data collection and location

We used forest-plot data from two main sources: (1) the Ecological Register, and (2) the AusPlots tall eucalypt forest permanent plot network. The Ecological Register (ecoregister.org; ~~Figure~~ Fig. 1) is a web/database resource that documents abundance distributions representing more than 2000 samples of plant and animal communities from around the world (Alroy 2015). Data are extracted from published literature. Forest inventories used in this study are based on diameter at breast high (DBH) lower cutoffs of 9.09 to 11 cm, with most cutoffs being exactly 10 cm. Of the 215 forest plots included in our analyses, 199 had estimates of species richness, 171 of basal area, and 214 of evenness. Site areas ranged from 0.025 to 40 ha, with modal value of 1 (*n* = 34), a median of 0.51, and a geometric mean of 0.49.

The AusPlots Forest Monitoring Network (ausplots.org) is comprised of 48 standardized one-hectare (100 × 100 m square) permanent plots in the tall eucalypt forests spanning the eastern, southern and western coastal regions of Australia. These plots were established between 2012 and 2015 as part of the Terrestrial Ecosystems Research Network (TERN), and included measurements of tree height, diameter at breast height (DBH), spatial location of every individual >10cm DBH, species identity and tree status (alive or dead; see Wood *et al*. 2016 for further details on the location, establishment and characteristics of each of the individual plots).



~~Figure~~ Fig. **1**: Location of the forest plots from the Ecological Register (http://ecoregister.org), and AusPlots (http://ausplot.org). Ecozones (Nearctic, Afrotropics, Neotropics, Australasia, Indomalaya) are represented by the areas within the dotted lines. The colour of the dots represent each habitat (tropical dry, tropical moist, temperate-mixed and coniferous).

Predictors of species richness

Generalized linear modeling framework

Generalized linear models (GLMs) were used to analyse the predictors of plot-based richness, basal area and evenness. The *a priori* predictors that could be applied across the plots worldwide were: mean annual temperature (MAT), mean annual precipitation (MAP), evapotranspiration (evap), latitude (lat) and 'habitat' (coniferous = 9 plots, temperate-mixed = 90, tropical-dry = 31, tropical-moist = 85; ~~Figure~~ Fig. 1). We estimated potential evapotranspiration (evap) from our MAT and MAP data using the equation of Komatsu et al. (2012).

To determine structural adequacy, the saturated additive combination of terms (i.e., ~ habitat + evap + mat + map + lat + lat^2) was first estimated using maximum likelihood in Program R. A quadratic term was used for latitude to account for the possibility that LDG are not centered at the equator (as the common approach of using the absolute value of latitude as a predictor implicitly assumes). Alternative family (gaussian, Gamma and inverse gaussian) and link functions (identity, log, inverse) were considered, and goodness-of-fit assessed (measured as percent deviance explained; %DE) when fitted to the global data set. This resulted in selection of the Gamma family for richness (log link, %DE = 68.3) and basal area (identity link, %DE = 21.5). For evenness (which is constrained between values of 0 and 1), the beta distribution was used, with a log link (%DE = 29.2). For the global and ecozone-based datasets, we considered the plot-level interrelatedness of the dependent variables by assessing the rank correlations.

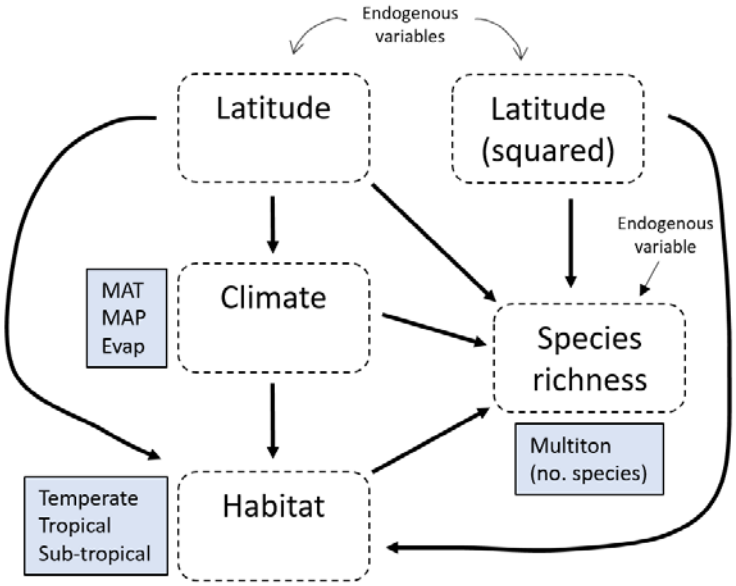
Five simpler linear models, representing alternative macroecological hypotheses, were fitted to the global dataset, with species richness, species evenness and biomass as dependent variables (depvar): (i) null (depvar has a constant mean across all plots); (ii) habitat (depvar depends on forest type, based on fitting to a four-level categorical predictor); (iii) evap (depvar is related to evapotranspiration at the plot); (iv) MAT + MAP (depvar depends on average temperature and precipitation at the site); (v) lat + lat^2 (depvar is controlled by latitude, reflecting a tropical-subtropical-temperate-boreal transition in either hemisphere). The same methods were applied to the dependent variables species evenness and biomass (SI). In each case, strength of evidence for a given model was assessed by its information-theoretic Akaike Information Criterion weights (with finite sample-size correction), AIC_c. In a second analysis, an additional biogeographic-climate categorical predictor, 'ecozone' was added to each of the models. Plots were aggregated into the Afrotropics (AFT = 35 plots), Australasia (AUS = 67), Indo-Malaya (INM = 33), Nearctic (NEA = 33) and Neotropics (NET = 34) zones. The plots (n = 13) that were not located in these five major ecozones were excluded from this second analysis.

Path Analysis

We performed path analysis (structured equation modelling without the use of latent variables) using the R package lavaan. Because path analysis rests upon linear modelling and does not allow for the use of tailor-made error distribution functions, we instead used conventional data transforms to normalize distributions – log (site area, stem density, and species richness) and square root (MAP and evap). Both the data from the Ecological Register and AusPlots were used in the path analyses. In

cases where Australia was separated, this simply refers to the AusPlots forest dataset, rather than the few Australian points that were in the Ecological Register. Many of the latter plots derive from Bradford *et al.* (2014).

Our main path analysis had four basic layers (~~Figure~~ Fig. 2). The dependent (endogenous) variables were species richness, evenness, stem density, and site area. All other variables were modelled as having direct effects on these four top-layer dependent variables. In summary, the completely independent (exogenous) variables were the biogeographic binary variables, latitude, and latitude squared. Note that to carry out the Australasian analysis, we had to drop the tropical moist broadleaf variable (no sites were in this category) and site area (all sites were the same size).



~~Figure~~ Fig. **2:** Conceptual diagram of the path analysis. The direction of the arrows shows the influence of one variable on another (i.e., dependencies and direct/indirect effects), and their order, on species richness.

Results

GLM framework

The saturated model (all terms: Lat + Lat^2, MAT + MAP, habitat, evap) explained 68.3% of the deviance (%DE) in species richness worldwide; model selection revealed the latitude^2 (quadratic) model was the best predictor (wAIC$_c$ = 1.00, %DE = 62.6). The saturated model explained 81.8 %DE for species richness in Australia, with latitude^2 again being the best predictor (wAIC$_c$ = 1.00, %DE = 79.6). By contrast, predictors of biomass and evenness were difficult to interpret at a global level, with much lower levels of deviance explained (Biomass$_{saturated}$ = 20.4 %DE; evenness$_{saturated}$ = 29.2 %DE). Furthermore, the best predictor for biomass and evenness at a global-level was different to species richness (Biomass = habitat: wAIC$_c$ = 1.00, %DE = 10.4 and evenness = Climate$_{MAT+MAP}$: wAIC$_c$ = 1.00, %DE = 25.2). Further details are given in the Supplementary Material (Appendix 2).

GLM: Ecozones and habitat

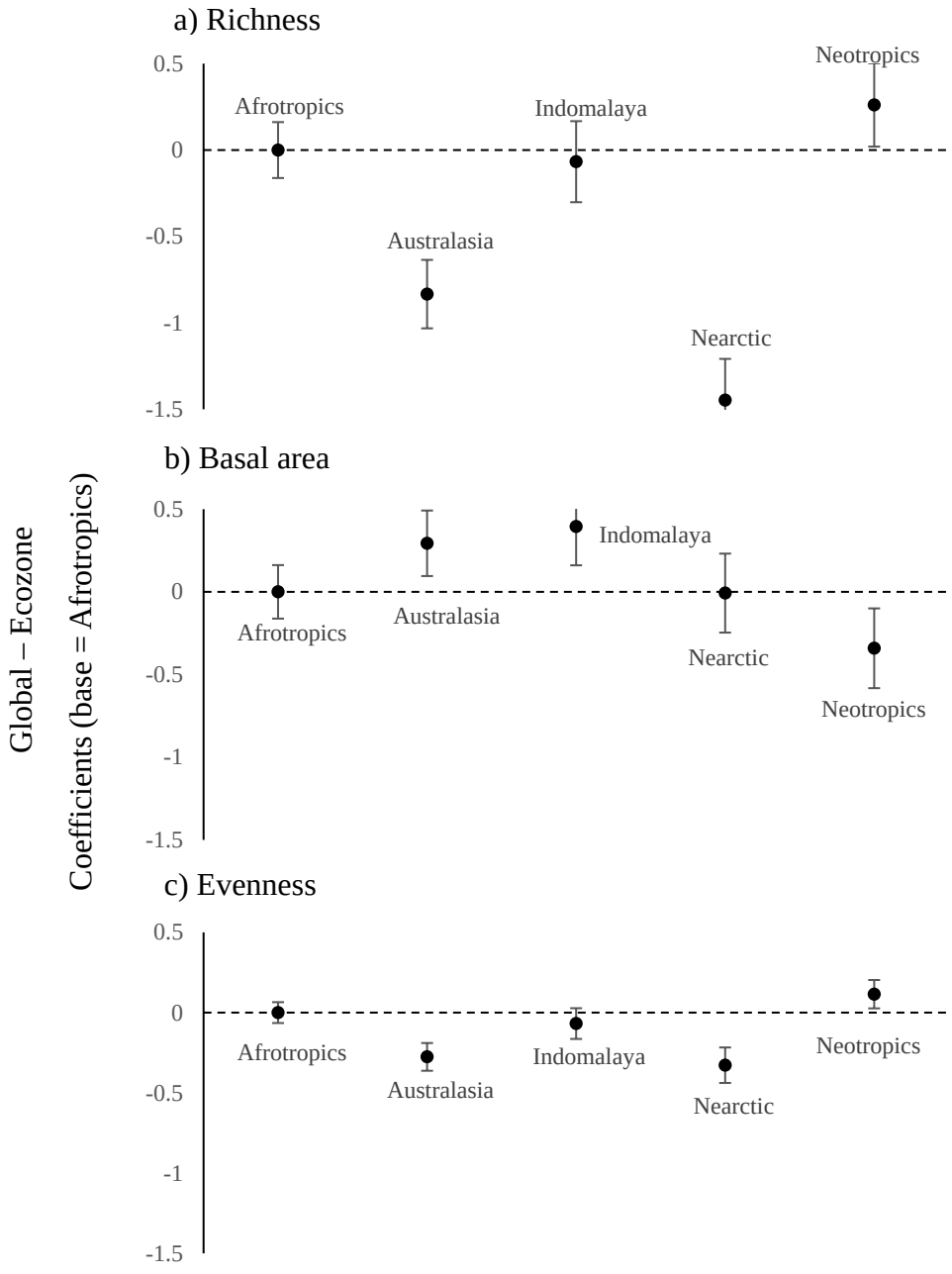
Forest plots in Australasia and the Nearctic had far fewer species, and lower evenness, compared to Indomalaya, Neotropics and Afrotropics (~~Figure~~ Figs. 3a, c); by contrast, biomass was similar across all global ecozones (~~Figure~~ Fig. 3b). Globally, tropical-moist habitats had the highest species richness, followed by tropical dry, temperate mixed, and coniferous (Table 2). Australia, by contrast, showed clear differences in biomass among habitat types – temperate mixed forests had the highest amount, followed by tropical moist then tropical dry (Table 1). Tropical dry and tropical moist forests were the most even in both Australia and the world (Table 1, 2).

Table 1: Coefficients of habitat (temperate-mixed, tropical dry, tropical moist) for Australia (using AusPlots forests). Including: the estimate, standard error, t-value and p-value.

Habitat	Estimate	Std. error	T value	Pr(>|t|)
Richness				
I: temp-mixed	1.64	0.08	19.40	< 2e-16
trop-dry	1.63	0.20	8.04	3.07e-11
trop-moist	2.02	0.17	11.86	< 2e-16
Basal area				
I: temp-mixed	4.20	0.04	99.12	< 2e-16
trop-dry	-0.58	0.11	-5.39	1.15e-06
trop-moist	-0.38	0.09	-4.45	3.60e-05
Evenness				
I: temp-mixed	-1.48	0.07	-21.12	< 2e-16
trop-dry	0.65	0.12	5.43	5.71e-08
trop-moist	0.65	0.10	6.24	4.41e-10

Table 2: Coefficients of habitat (temperate-mixed, tropical dry, tropical moist) worldwide (data source: Ecological register – excluding AusPlots). Including: the estimate, standard error, t-value and p-value.

Habitat	Estimate	Std. error	T value	Pr(>|t|)
Richness				
I: coniferous	1.38	0.32	4.29	3.52e-05
temp-mixed	0.95	0.35	2.75	0.007
trop-dry	1.92	0.37	5.14	9.97e-07
trop-moist	2.37	0.34	6.98	1.40e-10
Basal area				
I: coniferous	3.44	0.40	8.67	8.21e-14
temp-mixed	0.50	0.44	1.12	0.27
trop-dry	0.06	0.48	0.12	0.90
trop-moist	0.39	0.43	0.9	0.37
Evenness				
I: coniferous	-1.41	0.18	-7.71	1.31e-14
temp-mixed	0.22	0.19	1.15	0.25
trop-dry	0.50	0.20	2.52	0.01
trop-moist	0.51	0.19	2.70	0.01

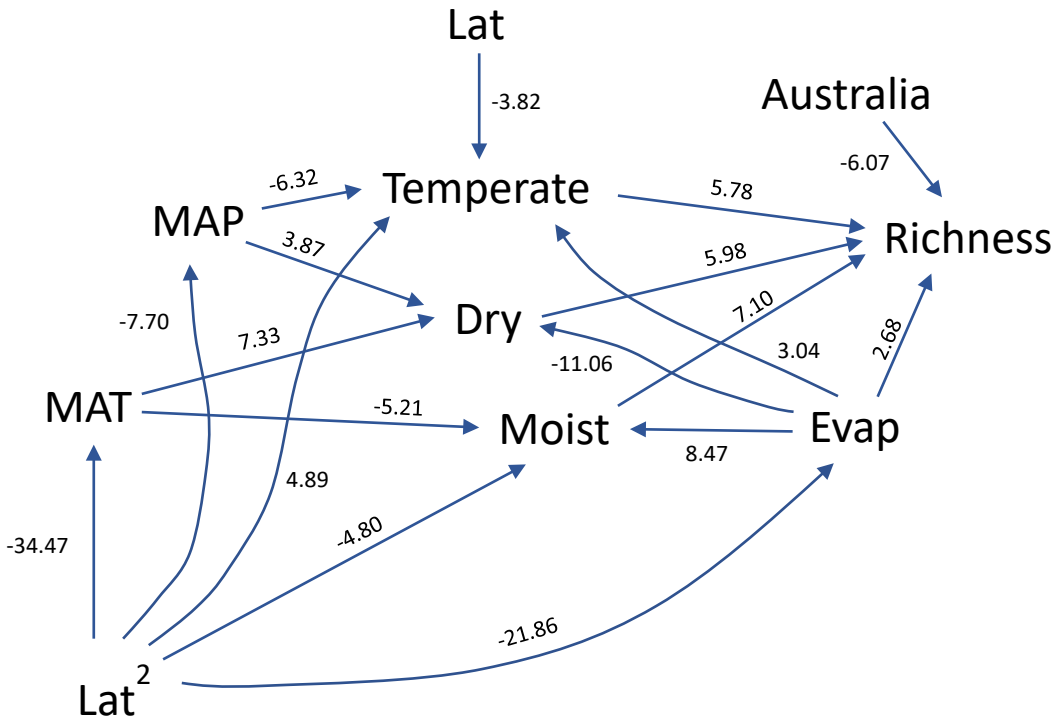


~~Figure~~ Fig. **3**: Coefficients of each ecozone (Australasia, Indomalaya, Nearctic, Neotropics) with Afrotropics as the intercept (data source: Ecological Register – excluding AusPlots) and error bars as the standard error associated with each coefficient.

Path Analysis

Species Richness

The structural equation model explained 75.9% of the variance in species richness (n = 195). Biogeographic effects (ecozone) were minimal, with latitude, latitude^2, MAT, and MAP by itself not being significant predictors (SI table X). Only five variables had significant direct effects at the $p < 0.01$ level: the Australian binary indicator (indicating that this region was qualitatively different to all others), the three habitat variables (temperate, moist, dry), and evap (Fig. 4). Additionally, there was significant covariance between richness and evenness, stem density, and site area (i.e., all top-layer variables covaried with richness). Basal area itself was not a significant covariate of species richness. Path analyses with the same structure were also carried out separately for the five ecozones (Table 3).



~~Figure~~ Fig. 4: Results of the path analysis showing the direction of influence of each variable on species richness (through variable dependencies) and their associated t-value.

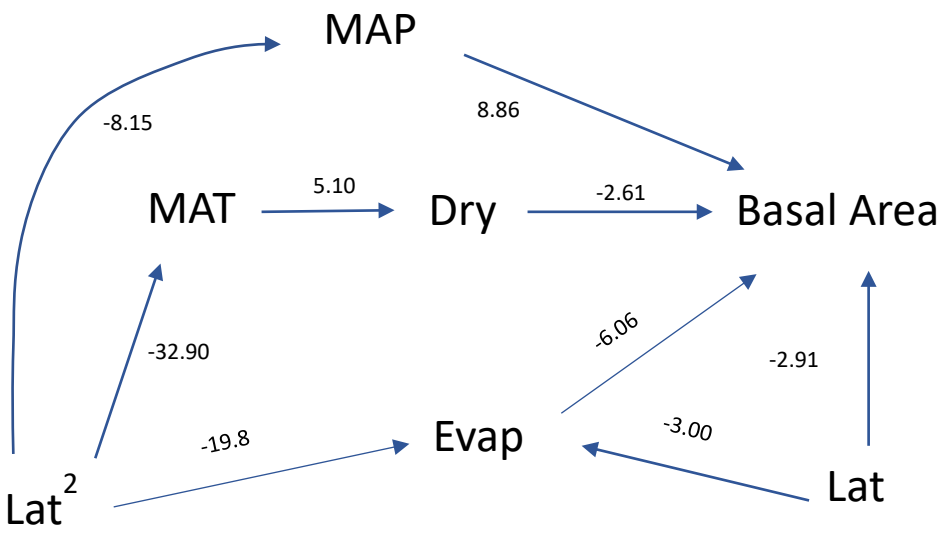
Table 3: Number of plots (*n*) and the variance explained (%) in species richness for each ecozone worldwide. Note that Australia in this table refers to the AusPlots forest database.

Biome	*n*	Variance (%)
Afrotropics	32	62.8
Australia	47	79.0
Indomalaya	29	56.4
Nearctic	31	45.0
Neotropics	26	36.6

The most variance explained in species richness was for Australia, with a clear effect of latitude ($p = 0.010$) and very nearly one for latitude^2 ($p = 0.011$). This result might be interpretable in terms of within-continent factors, such as the geographic isolation of southwestern Australia. The significant direct effects at $p < 0.01$ were MAP and evap for the Afrotropics. This result is difficult to interpret because it was not repeated in any of the other regional analyses. No individual effects were significant for the Indomalayan, Nearctic, and Neotropical data. It was also in these three biomes that we were unable to explain as much variance in species richness (Table X). However, the Neotropical data set yielded a marginally significant ($p = 0.056$) direct effect of the tropical moist broadleaf forest variable. This result suggests a role for seasonality, because seasonality of rainfall is the only obvious difference in the tropics between the dry and moist forest biomes apart from MAT, MAP, and evap, which were already accounted for.

Basal Area

Adding the logarithm of basal area to the structural equation model as another top-layer variable reduced the data set from 195 to 154 observations (some global plots did not report basal area). Variance explained increased to 80.8%. This change to the path analysis weakened the evap effect (*p* = 0.017) and introduced a north-south latitudinal gradient effect (*p* = 0.004), which is not to be confused with the equator-to-pole effect for which latitude^2 is a proxy. As reported in the previous section, the GLM analysis did suggest a latitude effect, regardless of whether evap was also included. We interpret this result as reflecting the indirect control of latitude on richness via the intermediate layers in our model: principally the biome and climate variables.



~~Figure~~ Fig. **5**: Results of the path analysis showing the direction of influence of each variable (and their relative dependencies) on basal area and their associated t-value.

Discussion

Forest biomes show a strong latitudinal gradient in species richness, from tropical regions containing diverse communities with many tree species, through to temperate and boreal systems that are typically dominated by one or a few canopy species (Pianka 1966). Our generalized linear modelling of species diversity in global plot data—spanning all forested continents and having been corrected for sampling intensity and plot size (via multiton subsampling: (Alroy 2017)—supports the general explanatory power of latitude. However, latitude is not, in itself, an ecological factor; it is a proxy for the underlying drivers of diversity and productivity. The question of what is *ultimately* causing the latitudinal effect in forest diversity, be it climatic drivers or a combination of abiotic and biotic influences, is of greater macroecological (Hawkins *et al.* 2004; Mannion *et al.* 2014; Pärtel *et al.* 2016). Our use of structured equation modelling, by exploring the path-dependency of a range of plausible predictors, revealed not only the direct, cascading and interactive effects of temperature, precipitation and evapotranspiration on biome type (and ultimately richness), but also the status of Australian tall eucalypt forests as an 'out-group' compared to other broadleaf/mixed forests worldwide.

Due to data paucity, past studies of forest-diversity gradients have missed Australia completely (ref), or else included only a handful of plots. Our analysis is the first to use data from the new and extensive AusPlots network (with a standardized protocol that samples a forest type [tall eucalypts] across its entire continental distribution in a global macroecological context (Wood *et al.* 2015). The latitudinal gradient prevailed in Australia, but unlike in the global data, the path analysis suggested that this was direct effect (i.e., not operating via its influence on climatic factors). When considered

alongside the distinct separation within Australia of the tropical, seasonal and temperate-mixed forest plots, this is suggestive of a role for biogeographic isolation. The Australasian realm had a long history of physical separation following the Cretaceous breakup of Gondwana (Fitzgerald 2002), and is today unique in its extensive, continental-wide distribution of tall coastal forests which have a canopy dominated by a single scleromorphic angiosperm genus (*Eucalyptus*). The continent dried progressively over the Neogene, leading to fragmentation of coastal forests separated by an arid interior (Martin 2006); these events seem to have created divergent adaptive pressures on the eucalypt forests, a legacy manifest today in the spatially heterogeneous and regionalized diversity-productivity patterns we observed in the AusPlots.

An overarching goal of macroecological analyses of species richness (and other measures of community structure and pattern in forests, such as basal area and evenness) is to draw generalities about the fundamental ecological and abiotic drivers of diversity and productivity (Pärtel *et al.* 2016). These results concerning diversity gradients in forests, based on the most comprehensive and sampling-intensity standardized analysis of plot data yet applied to this problem, reinforce the common-sense notion that latitude is an excellent 'top-down' predictor. What is also clear, however, is that this is largely due to its indirect influence on climatic variables, with consequences for availability of energy and water (Hawkins *et al.* 2003a), coupled with an eclectic mix of biogeographic peculiarities related to evolutionary history or region-specific details. The high variance explained (in the range of 50–90 %) by our climate-biome path analysis suggests that null models are not required to rationalize observed latitudinal diversity declines.

Practically, why should we care about the drivers of diversity-productivity gradients in global plant communities? Our results point to strong climatic controls on species richness, which is relevant to how forests worldwide will be shaped by anthropogenic climate change. Forest responses are likely to be driven primarily by global trends that induce a general latitudinal migration of ecosystems. However, our results also suggest that such shifts will be constrained by idiosyncrasies (e.g., relative isolation and regional differences in climate), interacting with socio-economic pressures like human use of land for agriculture and resources. This buttresses the notion that the protection and management of representative forest types across all continents and regions is important (Schmitt *et al.* 2009), because forests preserve unique packages of evolutionary history.

CHAPTER V

LOOK DOWN TO SEE WHAT'S UP: A SYSTEMATIC OVERVIEW OF TREEFALL DYNAMICS IN FORESTS

The study of treefall and its after-effects is a common theme in studies of forest structure and local dynamics, yet its value as descriptor of broader-scale ecological dynamics is rarely explored. Here we synthesize the most highly cited literature on treefall events, from 1985 to 2016 (in three-year blocks), highlighting the importance of their causes, characteristics and consequences. We then ask how this knowledge might contribute to the broader conceptual model of forest dynamics, and develop two conceptual models, which we use to illustrate both the classic and alternative views of how forests 'work.' Treefalls are one of the few 'integrating' attributes of forests, because of their ubiquity and longevity, and therefore can inform on a variety of processes (e.g., tree mortality, turnover rates, structural impacts, recruitment, and fire frequency) due to their impacts occurring simultaneously over space (patterns), and time (legacy effects). The substantial knowledge that already exists on localized

treefall dynamics should be combined with more integrative approaches to studying forest ecosystems, to investigate landscape-scale patterns of treefall and reconstruct past disturbance events.

Introduction

As threats to global biodiversity from land-use change and other anthropogenic influences (e.g., climate change) mount, the future of the world's forests has become progressively more uncertain. As a consequence, studies focussing on the impact and sustainability of activities associated with human development on forest biomes (e.g., logging, cultivation), and their interaction with the agents of global change (e.g., climate change, fire regimes, non-native species), have become prolific over the last two decades (Fridman and Walheim 2000, Siitonen 2001, Müller and Bütler 2010, Ganey *et al.* 2015). However, to forecast future forest distribution and biodiversity, it is also essential to have a comprehensive understanding of the eco-evolutionary forces that shape the structural features and dynamic processes that occur within forests (such as mortality, turnover rates, rate of treefall, canopy gaps, recruitment, nutrient cycling), as well as feedbacks between ecological and biophysical attributes.

Forest community composition and turnover are influenced by many ecological processes (Rogers 1996, Stachowicz 2001, Brooker *et al.* 2008). While some factors are consistently important and ubiquitous (e.g., climate, plant-plant interactions, mortality rates), others are spatially heterogeneous in effect and can be highly context

dependent (e.g., disturbance) (Orwin *et al.* 2006, Flower and Gonzalez-Meler 2015). However, forests are innately complex systems (Filotas *et al.* 2014), and strong interactions among processes can lead to reinforcing or diminishing feedbacks that are difficult to detect unless measurements over multiple spatial scales or temporal snap-shots are combined. These dynamic mechanisms cannot be studied effectively in isolation; moreover, the further back in-time we try to reach with our inferences, the more indiscernible the imprints of past processes become (e.g., legacy treefalls; McIntire and Fajardo 2009).

Much of the focus of the forest-ecology literature has been on the position, size and species identity of growing and mature trees, and the consequences of their removal (gap dynamics). Additionally, it is well known that trees can die standing, and remain in this 'state' for years as stags or stumps. As a forest attribute, stags and stumps are very important as they provide critical habitat for fauna (e.g., Leadbeater's possum, *Gymnobelideus leadbeateri*) and constitute an integral component of the forest structure (Franklin *et al.* 1987; Franklin et al., 1987). However, unless the wood is harvested, the tree will eventually fall to the forest floor, either immediately due to wind, or after a time lag due to age-related mortality.

This now-dead residue of the once-living forest is usually called 'coarse woody debris' (CWD), or treefall when the fallen log is still relatively intact. The age and volume of the dead wood contains signatures of past tree mortality, and so opens a temporal window through which we might perceive forest turnover rates, disturbance frequency, die-off events, past recruitment pulses and species-trait responses. For example, the presence of heliophilous species in an old-growth forest may be indicator

of past disturbance, which enhanced light availability by opening canopy gaps (Ulanova 2000) . In systems where decay rates are slow (e.g., cool-temperate or boreal forests) or regions where disturbances such as fire are rare, the fallen wood can persist for decades to centuries (Siitonen *et al.* 2000), thus providing a long-term record of change in the forest.

Yet there remains ambiguity about the structural effects of treefalls on the spatial distribution of the living components of forests at different scales (You *et al.* 2012). Is treefall a forest attribute worth studying for its intrinsic ecological value, or in the overall context of forest dynamics, is its importance defined by how it opens canopy gaps for the recruitment, growth and competition of new living trees? The current definition of a treefall typically relates to the size, frequency and purported causation of the fallen wood (e.g., windthrow or blowdown, forest or canopy gap, or average size and density of the CWD). However, ecologically, treefalls might equally refer to both structural characteristics and temporal features simultaneously, including the dead (but still standing) trees, the act and consequences of a tree falling, the fallen log on the forest floor, and the legacy effects (e.g., past physical displacement of large trees, root pits and mounds) that persist as an imprint after the dead wood has decayed.

Here we present a systematic overview of the last three decades of refereed literature on treefalls and dead wood, and show that although treefalls have been repeatedly demonstrated as important facilitators of forest structure and process, their relationship to the living components is usually overlooked or implicitly downplayed. Most studies have focused solely on the effects in their immediate proximity. Specifically, we sought to: i) examine the causes, characteristics and important consequences of

treefalls, drawing attention to current gaps in our knowledge of treefall events; ii) critically evaluate the importance of treefalls as key components of forest ecological processes; iii) highlight areas for future study, including a re-evaluation of the conceptual model of forests when treefall is given explicit priority (and measured regularly and systematically, alongside attributes of the living forest). In pursuit of our final aim, we compare an example of a classic model of forest dynamics (traditionally focused on the life cycle of a tree) with an alternative approach, where tree death and treefall are seen as complementary windows into hidden underlying ecological processes.

Methodology

To sample the literature representatively, we undertook a series of searches using different combinations of key words relevant to treefall, disturbance, woody debris and forests (for example: TS = (treefall AND log AND forest); TS = ("fallen tree" AND log AND forest); TS = forest AND ("coarse woody debris" OR CWD); TS = (forest AND disturbance AND dead trees AND stumps, etc.)). The subsequent references and citations in the most highly cited of these papers were also scrutinised. We then combined the results and cross-referenced across the searches to remove duplicates, leaving a useable tally of ~ 2,500 papers. To ensure a comprehensive yet tractable synthesis of this literature, we then created two summary tables, one that listed the most highly cited literature from 1985 to 2016 (separated as sequential three-year blocks; SI Table 1; 73 papers), and another (Table 1; 25 papers) that focused on four examples (not duplicated in SI Table 1), representing each of a classic, well-cited,

review/meta-analysis, and recent study (published within the last two years). Our choice of categories for grouping the selected papers was dictated by the most common themes that were covered in the literature. These were: i) **causes** of treefall; ii) **consequences** of a treefall and; iii) **characteristics** of the fallen tree and the landscape, which is typically influenced by i) and has an effect on ii) (Fig. 1.). Within this ecological context, for SI Table 1 we broke the studies into six categories within each of the three-year blocks, being: (a) canopy gaps, (b) decay and nurse logs, (c) extreme-weather events and disturbance, (d) modelling and forest management, (e) non-living and structural effects, and (f) tree mortality and standing dead.

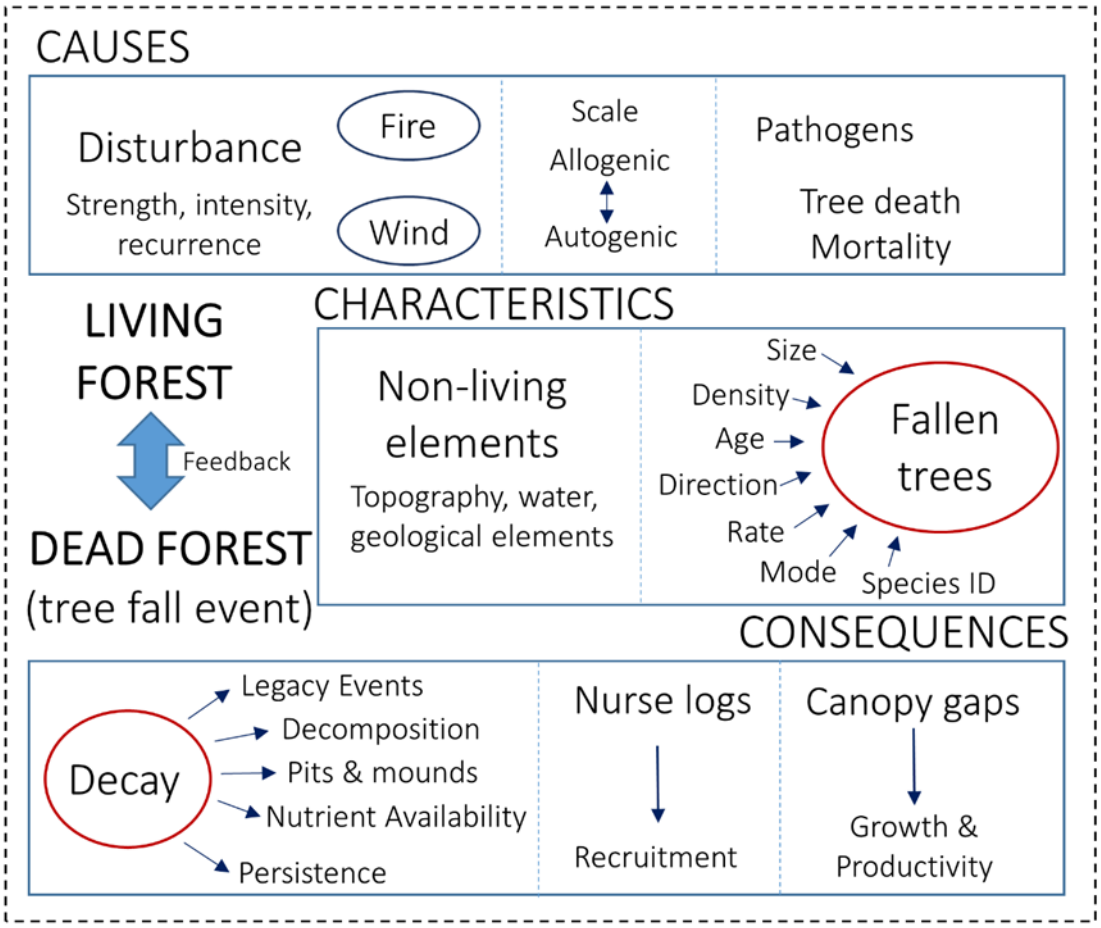


Fig. 1: Summary of the most commonly studied research themes in the treefall literature (broken down by the categories shown in Table 1). Each theme relates to

whether the study predominately explored the causes, consequences, or characteristics of the treefall.

Treefall literature: current knowledge

The most common terms used in the literature across all groups included ‘gap(s)’, ‘coarse woody debris’ and ‘treefall’ (Table 1). These terms were often used interchangeably and were chosen/defined at the researcher’s discretion, depending on the question or the main finding (e.g.,Guby and Dobbertin 1996, Soderberg *et al.* 2014). Field measurements and observations were the most common type of study, and these were predominately done at an individual- to community-level (Table 1). For the papers that were included in this research synthesis, ecosystem and landscape-scale investigations included mainly reviews, meta-analyses or syntheses as these were the most likely to be heavily cited (Table 1).

Table 1: Contextualisation of the dead-wood forest literature, categorised into four major research themes: causes of treefall, characteristics contributing to propensity of a tree to fall, consequences of a treefall event, and management or modelling applications. The papers that that were included in each category were chosen to represent the following four criteria: i) a 'classic' study (for historical grounding), ii) a highly cited example, iii) the most recent published review, and iv) a recently published study based on primary research.

Author(s)	**Forest type**	**Topic of paper**	**Study type**[^]	**Impact**[*]	**Key development/finding**	**Cites**	**Terminology**
CONSEQUENCES ***Canopy gaps and gap dynamics***							
(Brokaw 1985)	Tropical	An assessment of Watt's (1947) description of mature forests as shifting mosaics & gap size dependence of regrowth using periodic observations at multiple sites.	FM	P	Accordance with Watt (1947): Gaps of different sizes and stages of regrowth are an important source of heterogeneity in composition and dynamics of tropical forests.	821	Treefall gaps
(Uhl *et al.* 1988)	Amazon forests	Effect of gap microhabitats on nutrient availability and regeneration, and the role of gap size in influencing regeneration within a gap within 4 years after gap establishment.	FE & FM	C	i) Treefall gaps principally benefit pre-established seedlings and saplings, ii) gap size has little effect on plant density, establishment and mortality, and iii) gap microhabitats have negligible effects on vegetation dynamics and nutrient availability.	398	Treefall gaps

(Muscolo *et al.* 2014)	All forest types	A review of the roles of forest canopy gaps.	R	P	To further understand the impact of gaps on the forest as a whole, further investigation needs to be done on the below-ground communities (including: soil processes, organic matter trends, composition and activity of the microbial biomass, and soil characteristics).	3	Treefall gap
(Zhu *et al.* 2014)	All forest types	Meta-analysis on the effect of gaps on woody-plant regeneration.	M	E	Overall, forest gaps enhance woody plant regeneration, and the effects of gaps varies with forest type, gap characteristics, environmental factors and plant traits.	8	Forest gaps & treefall gaps
CAUSES ***Disturbance (Extreme weather events [fire & wind], uprooting)***							
(Canham and Loucks 1984)	Hardwood forest	Assessment of the frequency and extent of catastrophic windthrow, and identification of the mechanisms.	FM	P	Return time for a catastrophic windthrow in these forests is 1,210 years with catastrophic thunderstorms as the principle mechanism for large-scale blowdown.	379	Blowdown & windthrow
(Attiwill 1994a)	All forest types	A review of the literature on natural disturbances in forests.	R	P	An ecological framework of natural disturbances and its component processes and effects is synthesised and developed in this review. Provides the basis for sustainable forest management.	798	Tree fall

(Ulanova 2000)	Boreal forest	A review of the literature on the ecological effects of windthrow and its effects on forest structure and composition at differing spatial scales.	R	L & C	The creation of gaps and microsites by windfall disturbances are two related major environmental components determining the regeneration niche of forest plant species. Windfall disturbances also increase biodiversity (for further information on how, see the paper).	310	Gap-phase dynamics, windthrow & fallen tree
(Šamonil *et al.* 2010)	All forest types	Investigation of the reported roles of tree uprooting in soil formation.	R	E	Knowledge on the effect of tree uprooting on soil formation is well understood across multiple scales, but there is limited quantitative data to date supporting much of the theory.	55	Tree uprooting
(Bassett *et al.* 2015)	Eucalypt forest	Development of a conceptual model of CWD dynamics pre- and post-fire to predict how topography, fire severity, and fire history interact to affect the availability of CWD in forests.	M	L	Both fire severity and fire frequency influenced CWD availability in gullies, where CWD on slopes was not. Gullies generally supported more logs than slopes, but longer inter-fire intervals in gullies may allow fuel loads to accumulate and lead to comparatively larger fire impacts.	2	CWD & logs & dead trees
CAUSES ***Tree mortality & Standing dead***							
(Franklin *et al.* 1987)	All forest types	Description of tree death as an ecological process.	R	I to P	Tree death demonstrates key principles of ecological process, and defining the spatial and temporal context of the study is important.	683	Tree death

(Fridman and Walheim 2000)	All forest types	Evaluation of the dead-wood inventory in Sweden.	FM/M	C	Logs are more decayed than stags. Forest management affects the amount of dead wood present, less dead wood using clear-cut and thinning methods. Inventories are important and are usable as a tool for assessments of dead wood.	403	Dead wood, standing dead
(Lugo and Scatena 1996)	Rainforest	Causes and consequences of tree mortality.	R	C	Tree mortality events vary extensively across time and space. These events often differ depending on stand conditions, and stem densities (higher mortality with higher densities). Ecological impacts of a sudden tree mortality event contrast with gradual background mortality.	28	Tree mortality, tree fall gaps
(Soderberg *et al.* 2014)	Boreal forest	Assessment of the choice of definition on the amount of dead wood that is reported.	FM	C	The differing definitions of 'dead wood' used in studies substantially affects the quantity of dead wood that is reported - in most cases leading to underestimates of dead wood volume.	1	Dead wood
CONSEQUENCES ***Decay & nurse logs (recruitment)***							
(Sollins 1982)	Douglas-fir forest	Decay rates and turnover in an old-growth forest, assessment of previous measurements that may have been misleading.	FM	C	Densities of fallen boles are lower than previously reported due to methodological and field measurement differences. Highlights the value of permanent plots (undisturbed) for	330	Tree mortality, fallen boles, fallen and standing dead woody material

					accurate representation of decomposition and nutrient dynamics.		
(Siitonen *et al.* 2000)	Norway spruce forest	Differences in stand structure between managed and unmanaged stands (comparing mature and old-growth).	FM	C	Average volume of CWD was much higher in old-growth (managed) than mature (managed) and over mature stands. Logs contributed the most to CWD volume.	376	Coarse woody debris (CWD), living trees, logs, dead standing trees
(Weedon *et al.* 2009)	All forest types	A global meta-analysis testing the hypothesis that interspecific differences in wood traits affect decomposition of woody debris.	R	E	Found support for their hypothesis. Gymnosperm wood decomposes more slowly that angiosperm and key nutrients such as nitrogen and phosphorus correlate with decomposition of angiosperm woody debris.	152	Woody debris
(Cousins *et al.* 2015)	Mixed conifer forest	Developing understanding of the decay rates of standing dead tree and the implications for carbon accounting in forests.	FM	C	Carbon density of the most decayed SD trees was 60% that of live trees. Species ID, SA:Vol ratio and relative position within the tree are all important characteristics that explained the SD patterns.	1	Standing dead (SD) trees, woody debris, deadwood
CHARACTERISTICS ***Non-living & Structural Elements***							

(Maser 1984)	All forest types	Synthesis of the available data on fallen trees in unmanaged forests with the aim of highlighting the research needs and knowledge gained.	R	E	There is a lot that we do know about fallen trees and fallen trees are important! Research needs to focus on comparisons between managed and unmanaged stands, as the physical qualities of a fallen tree (such as moisture, temperature, nutrient etc.) are likely to vary. More particularly, what do changes in and around the fallen tree have on the overall functioning of ecosystems. Soil-log interface is important.	327	Fallen trees, wood, woody debris
(Harmon *et al.* 1986)	Temperate forests	Describes CWD and its flow/movement into, from and within an ecosystem.	R	E	Rates of input/accumulation of CWD in forests ranges from 0.12 to 30 Mg/yr. This input depends largely on the size of the tree (rate of decomposition), and frequency of disturbances (particularly big ones!). CWD mortality is expected to be aggregated (due to the processes governing tree death such as wind, pathogens affecting multiple individuals of the one area).	3166	Woody debris, coarse woody debris (CWD), dead trees, downed boles, logs
(Woldendorp and Keenan 2005)	Australian forest	Assessment and literature review of CWD in Australian forests.	R	E	CWD can be high in exotic pine plantations if substantial amounts have remained from the once native forest. There were differences in CWD quantity depending on stand age; young <20yrs = lowest percentage of CWD, older >70yrs = highest CWD and stag biomass. Tree size influences CWD amounts (i.e., tall open forests CWD much greater because of taller trees).	67	Coarse woody debris (CWD), standing and fallen dead wood, snags

(Oberle *et al.* 2015)	Temperate forest	Importance and movement of deadwood after treefall.	FM	C	While logs can fall in many different directions; Snags, logs and branch average direction was consistent with downhill deadwood movement as trees fall. Relationships between log and landscape attributes (movement, shape and topography) suggest that downhill rotation during treefall drives most of the deadwood distribution over their study site.	1	Logs, deadwood, snags
APPLICATION ***Modelling & Forest Management***							
(Lorimer 1985)	All forest types	How to infer past disturbance dynamics without using destructive techniques and using more than just age of trees.	R/M	P	Currently, it is difficult to identify past disturbance (severity) from the distribution of tree among age-classes. They advocate that to study disturbance history, random dispersal of plots of various size across a large land area is recommended.	280	
(Siitonen 2001)	Boreal forest	Exploring the relationships between CWD, forest management (intensively vs. unmanaged), and saproxylic species.	R	E	In managed forests, the average amount of CWD in the landscape has reduced by 90-98%. General species area relationships suggest that a reduction in available habitat (i.e., as logs), might lead to a reduction of > 50 % saproxylic species in the long term. It is important to assess how much CWD should be retained in managed forests.	904	Coarse woody debris (CWD), dead tree, decaying wood

(Schliemann and Bockheim 2011)	All forest types	Review of the inconsistencies in gap terminology, and the methods and modelling used to investigate treefall gaps and the influence of gaps in a forest system.	R	E	Recommends a range of standard protocols when studying treefall gaps. E.g., the size of treefall gaps varied across studies; this study suggested a maximum gap size of 1000m2 (gap size can influence the results due to scale dependencies of processes). Gap shape varies and should be determined through extensive field survey.	70	Treefall gaps, canopy gap
(Fisher *et al.* 1991)	All forest types	Description of the development of the individual-based & process-based forest gap model FORMIND and its potential application to tropical forests.	M	E	Long-term modelling projects not only provide understanding of forest systems, but also provide benefits for ecological theory and empirical study design. They are powerful tools, and are becoming increasingly valuable in today's research.	0	Forest gap

Causes

Mortality of trees was a central focus of the literature across all categories (Table 1) and disturbance events were considered the main drivers of treefall (Attiwill 1994a; Christensen *et al.* 2005). While plant senescence leads trees to be more susceptible to biotic and abiotic factors, the death of the entire individual does not occur often without an external disturbing agent (Franklin *et al.* 1987). Fire, extreme wind events and knock-on effects to neighbouring living trees by a treefall event are common examples. It follows that the characteristics of treefall events are strongly correlated with type, magnitude and frequency of disturbance (Jonsson and Dynesius 1993). For instance, the severity of wind damage can vary from the death of a single tree to extensive windthrow (Canham and Loucks 1984), depending on storm intensity, timing, and its interaction with local conditions, tree size, and species involved (Everham and Brokaw 1996; Rich *et al.* 2007). Similarly, the interplay of fire regimes (frequency and intensity) and topography—which affects fire behaviour and fuel load—determines the extent of tree damage and recovery time (Bassett *et al.* 2015). Disturbance characteristics also influence the spatio-temporal distribution of standing and fallen dead wood (Harmon *et al.* 1986; Lugo and Scatena 1996) and consequently treefall analysis can be a non-invasive technique for reconstruction of disturbance history and tree death.

Characteristics

Depending on tree size, treefall can occur through trunk snap or tree uprooting, the latter of which determines the formation of pit-and-mound microtopography (Peterson and Pickett 1991). At a fine scale, the common view is that pits and mounds inhibit soil development. For instance, Ulanova (2000) found that microsites characterised by

pit-and-mound topography differ pedogenically from undisturbed soil, and the time required for soil profile to recover was directly related to uprooting depth. Microsites can display significant differences in light, soil moisture and temperature (Peterson *et al.* 1990), and their extent is directly related to tree size (Sobhani *et al.* 2014). However, at the scale of a forest ecosystem, the impact of tree uprooting on soil spatial variability is still poorly understood and more quantitative data are required to fully comprehend the ecological consequences of this phenomenon (Šamonil *et al.* 2010).

Dead trees themselves also provide, through accumulation of coarse woody debris, a sizeable fraction of a mature forest's stored carbon (biomass), and nutrient budget (Franklin *et al.* 1987). Consequently, CWD quantity, quality, and decomposition rates have a crucial influence on nutrient cycling, because large amounts of organic matter are transferred in the soil and/or in the atmosphere (Harmon *et al.* 1986). That said, the total amount of CWD in a given forest varies greatly with species composition, stand age, tree size, temperature, and humidity (Woldendorp and Keenan 2005; Weedon *et al.* 2009). Moreover, landscape features such as slopes and valleys affect CWD spatial distribution and decomposition, with logs tending to move downhill where they are also susceptible to more rapid decay (Oberle *et al.* 2015; Zanne *et al.* 2015).

Consequences

The creation of a canopy gap is arguably the most obvious consequence of treefall in a closed forest. Accordingly, the most common and highly cited research category in the literature on treefall was canopy-gaps and gap-dynamics (Table 1, Table S1), with 50% of papers focussing on this topic alone (e.g.,Brokaw 1985; Whitmore 1989;

Canham *et al.* 1990; Arevalo and Fernandez-Palacios 1998). Depending on their characteristics—particularly size, shape, distribution, and age—canopy gaps introduce environmental heterogeneity locally, determining changes in light levels, soil nutrient availability, litter depth, belowground competition and spatial patterns in regeneration at a landscape level (Bowman and Kirkpatrick 1986; Muscolo *et al.* 2014). These effects have been recorded in both temperate and tropical forest environments (Canham *et al.* 1990), although with exceptions, which were predominantly focused on single-treefall gaps in any forest (e.g. Uhl *et al.* 1988). The microhabitats generated by canopy gaps enhance plant regeneration, with the magnitude of this effect depending on forest type, gap characteristics, local conditions and plant functional traits (Zhu *et al.* 2014). Gaps can result in: (i) increases biodiversity by facilitating the establishment of pioneer, shade-intolerant species, (ii) rejuvenation of the gene pool, since gaps are mostly colonised by seeds and spores, and (iii) enhanced structural complexity, as species are represented by individuals at different life stages (Brokaw 1985; Attiwill 1994a; Ulanova 2000; Muscolo *et al.* 2014). Gaps can be more or less important depending on the regeneration regime and forest type. For example, in continuously regenerating tropical forests, light is extremely limiting, and gaps here provide regeneration 'pulses' that would not otherwise occur without the gap (Brokaw 1985). Conversely, Australian tall Eucalypt forests predominately regenerate via a stand-replacing disturbance event and rely less on the continuous availability of gaps (Attiwill 1994b), although gap size have been correlated with regeneration success in *Eucalyptus regnans* stands (Van Der Meer *et al.* 1999). Despite the influence of canopy gaps on local conditions, both terminology and field work protocols are still inconsistent between studies and therefore results can be difficult to interpret and compare (Schliemann and Bockheim 2011).

Other than creating a gap in the canopy, the physical presence of fallen logs also facilitates plant establishment for some tree species, particularly at advanced stages of decay when stored nutrients are more readily accessible release (Harmon *et al.* 1986). Nutrients and water are released slowly from CWD and hence, when CWD is not removed, they are retained in the ecosystems until plant productivity recovers (Harmon and Hua 1991). However, these dynamics are still poorly understood and results from different studies can be contradictory, or relate to very different process such as seedling establishment versus nutrient dynamics. For example, mounds and decaying wood has been found to be important substrates for the germination of the coniferous species *Picea abies* (Ulanova 2000, Zielonka 2006), but a study on meso-eutrophic forests found that only one of nine species investigated displayed higher seedling density on logs, suggesting that differences amongst species (in trait characteristics, presence or absence of mycorrhizal associations, for instance) might also play an important role (Chećko *et al.* 2015). Furthermore, Laiho and Prescott (2004) inferred only a limited role for CWD in the nutrient cycle of north coniferous forests. The positive effect of fallen logs on seedling establishment could then be due to the lower competition with herbs and mosses occurring on CWD compared with soil, and only partially to enhanced nutrient availability (Harmon and Franklin 1989). The presence of decaying wood is also crucial for organisms other than plants, such as bryophytes and saproxylic fungi and invertebrates, which rely on spatio-temporal continuity of suitable host trees for their persistence in the forest community (Siitonen 2001).

Living-forest dynamics

In models the dynamics of a forest classically begins with recruitment and seedling establishment, through growth, maturity and reproduction of the canopy tree, and ends with its death and eventual fall (Franklin *et al.* 1987). Over time, the fallen log decays, with this process in turn facilitating many important ecosystem services across space and time, including recruitment (as a nurse log, or via gap-dynamics), decomposition (nutrient turnover, microbial community growth and diversity), habitat for animals or bryophytes, and structural influences on the pattern and growth of living trees; so the cycle begins again (Fig. 2).

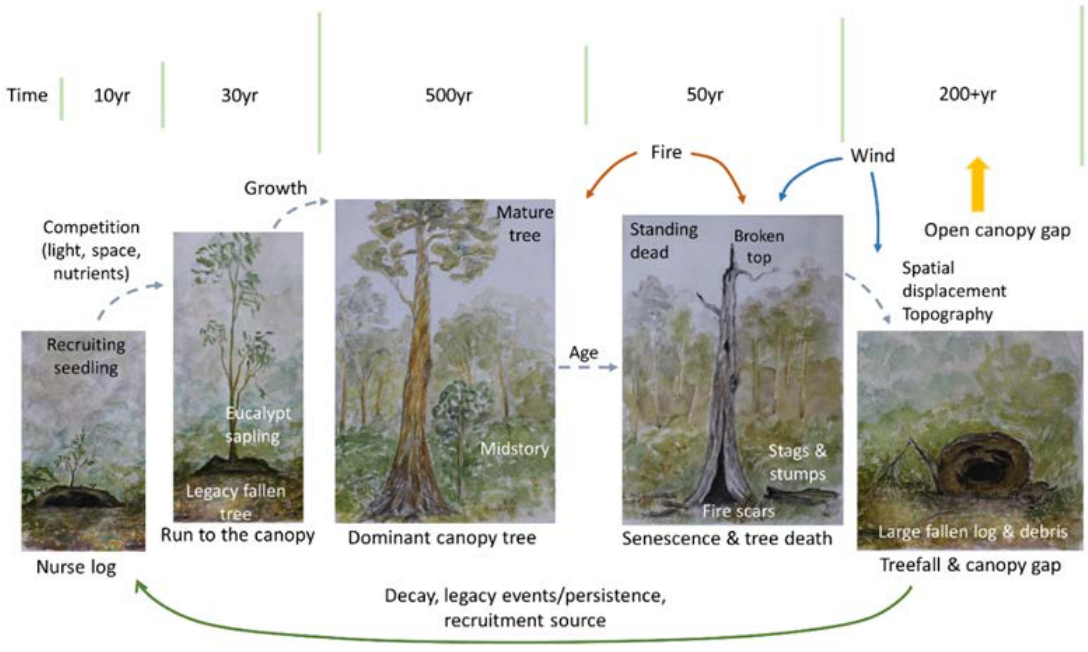


Fig. 2: Example of a classical model of forest dynamics, in the context of canopy trees. It begins with recruitment and growth, and ends with treefall and log decay. The direction of the arrows show movement between states, and where key forest processes may be occurring. The green bars indicate duration of stages—in the case of a stand

replacing event, the forest may transition from a living tree, or a stag, directly to regeneration following fire. In these circumstances however, it is unlikely that the fire will result in 100% removal of CWD.

Additionally, treefalls are obvious indicators of disturbance events (e.g., Van Der Meer and Bongers 1996). In this context, it is apparent that an important driver of change and structure in this classical tree-focused conceptual model of a forest is the 'dead' component—and the dynamical processes that it facilitates. We recognise two defining and inseparable features of forests; the 'living' (seedlings, saplings, mature trees) and the 'dead' (stags, fallen logs, etc.). The transition between these states needs a stimulus, making a disturbance event (e.g., wind, fire, pathogens) and time, the key to maintaining this dynamic flux (Fig. 3).

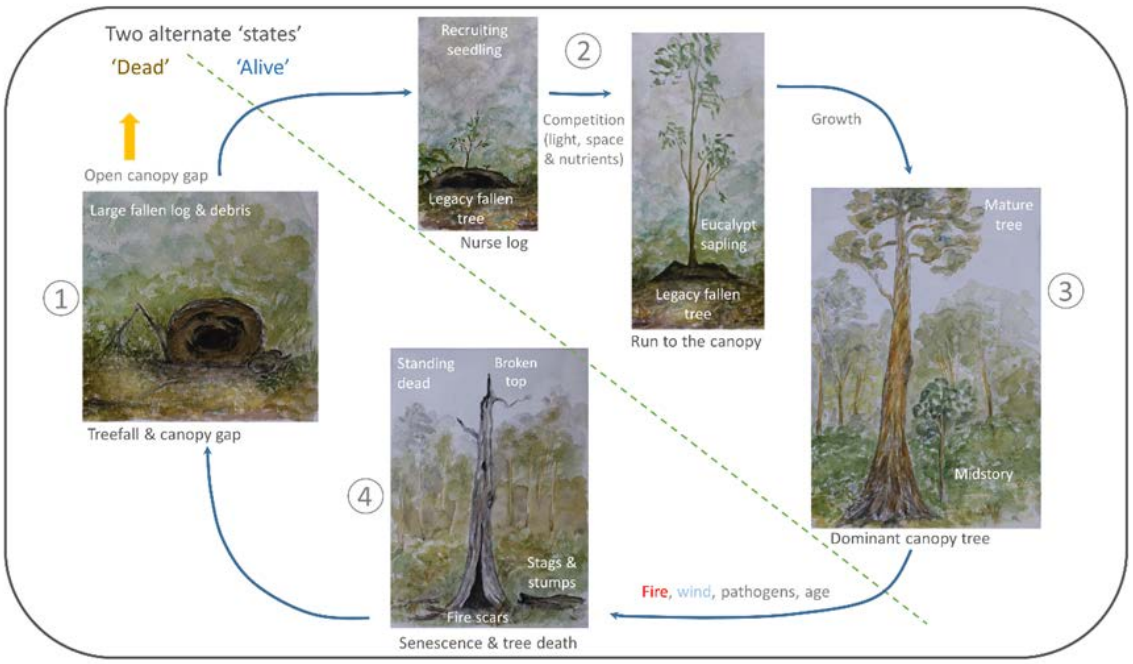


Fig. 3: Example of an alternative conceptual model of forest turnover (c.f. Fig. 2), with large fallen logs (the 'dead' components of forests) as the central focus. The two alternative states of forest turnover are separated by the dotted line, and includes the 'living' (with the mature tree as the 'end' point of the 'living' state) and the 'dead' states. The direction of the arrows show movement from one state to the next (with the key processes involved in the movement between states written above the arrows where required). This image is conceptually similar to Fig. 2, but depicts both stages being equally as important to the structure and dynamics of an example forest. Disturbances such as fire, wind, pathogens and age are key to the transition into the 'dead' state, where canopy gaps, for example in tropical forests, are the key to unlocking continual regeneration of the living state.

A treefall's eye-view of a forest – What is next?

When looked at from the perspective of treefall, the prevailing state of a forest centres on dead components; standing-dead trees, coarse-woody debris and fallen logs, which typically persist for much longer than it takes for a seed to establish, compete, and race to the canopy. From the perspective of the dead tree (fallen log), the living forest is arguably more unstable and in a constant flux, depending on inputs, environmental conditions (determining decay rates) and disturbance (fire, wind). Observations and measurements of the dead states (in particular, the size, spatial position, decay state and fire scars of a fallen log), can provide a powerful tool for inferring deeper-time eco-evolutionary processes—reaching much further back than the relatively evanescent information provided by observations of only the living components would allow (Swetnam 1993; Boswijk *et al.* 2014). As such, the analysis of treefall allows us to look back into the past using snap-shot patterns and log dating, and so measuring the attributes of the dead forest offers a crucial augmentation to measurements of the sizes, identities and positions of the living trees. Yet the measurement and use of the spatial locations of treefalls remains underexploited in plot-based studies, based on our survey of the literature (Table 1 and Supplementary Material, Appendix 3). A more explicit focus on the causes and consequences of treefall as more than just 'an opener of canopy gaps' might also be useful for improving pattern-oriented models (POM) of forests (Wiegand *et al.* 2003). This is because analysis of the patterns of the fallen wood should permit an explicit filtering and verification of the adequacy of structural forest models that seek to characterise the interplay between living and dead forest components, and broader community dynamics.

Future directions

The relative stability of the dead component of a forest is largely context-dependent (i.e., tropical versus temperate forests). However, its unresponsiveness to short-term fluctuations in environmental conditions, allows information on past events and dynamics to be preserved through time. But to properly identify and contextualise the importance of treefall as a key forest process, integrative modelling (e.g., POM) is a necessary approach (Grimm *et al.* 2005) because it allows for an explicit mechanistic view of functions and feedbacks, as well as permitting sensitivity analysis of key parameters and scenario testing. For instance, a forest represented *in silico* (e.g., the BEFORE model; Rademacher *et al.* 2004) can be used to manipulate treefall frequency, density and occurrence patterns, and assess the role of treefalls in determining equilibrium dynamics, disturbance and the spatial positions and/or growth of living trees, via a simulation that encompasses anything from a cohort of canopy trees through to a model of the entire forest community or ecosystem. Further, using 'bottom-up' model verification, such as POM 'filters' to pattern-match and test the influence of multiple predictors on observations (e.g., treefall, in combination with other biotic and abiotic processes such as competition, facilitation, fire, humans), future 'simulation experiments' could allow for testing the sensitivity of processes and centrality of treefall in shaping the character and definition of a forest (e.g., probability of a phase transition into an alternative state, such as a degradation into open vegetation or continued thickening into a heavily closed, continuously regenerating, and gap-dependent system). This type of modelling approach might also help underpin decisions on the resolution and ecological basis of the structural thresholds currently used to define and characterise what a forest is, i.e., what is the biological basis of

current thresholds of >10% canopy cover at 5 meters in height and covering an area of at least half a hectare? (Food and Agriculture Organisation 2012).

Two of the key advantages to characterising the metrics of treefall in forest-plot protocols are: i) the literature already contains ample information on the importance and function of treefalls in forest communities (Table 1, Supporting Information); and ii) because a treefall is relatively easy to observe (it can be readily seen, and measured) and persists (in the absence of fire) in the landscape, researchers can take advantage of mensurative experiments (e.g., patchy landscape fires) to infer temporal dynamics of a system based on 'snap-shot' patterns. For example, studies comparing different forest types with matched pairs that are either undisturbed or selectively logged (i.e., living trees remain intact but fallen logs are removed), or treefall-frequent (continuously disturbed) versus treefall-infrequent forests, assesses the importance of fallen and legacy wood in shaping the structure and dynamics of a forest (Maser 1984). Additionally, uncovering which forest species benefit most from treefalls, and how treefalls fit in systems that are heavily reliant on mass disturbance and regeneration, could also be a key direction. In short, all of these ideas are scientific and testable.

Of course, measuring and modelling the dynamic components of forests (e.g., treefalls) will, in some cases, be infeasible. For instance, mapping the size and position of potentially hundreds of fallen logs per hectare is a significant logistical undertaking. Furthermore, the reliability of LiDAR and remote sensing in the spatial analysis of treefall is, although promising, yet to be fully developed, particularly for what concerns logs (Wing *et al.* 2012). The relative information that can be gained from treefall in any given forest will depend on a variety of factors, like climate, fire

frequency, decay rates, and so on. Such factors will principally influence the rate of transition between the states. For instance, in warmer, drier forests, the frequency of fire and activity of termites will typically be high, removing any lasting legacy of the fallen trees (reaching an extreme in the tropical savannas). This contrasts strongly with cool, wet rain forests, where ancient logs on the forest floor are among the most persistent feature of the ecosystem, shaping its dynamics across time scales that last much longer than a typical plant lifespan (Sollins *et al.* 1987; Vanderwel *et al.* 2006).

The relative importance of treefall to a given forest's dynamics might also wax and wane over time, and in situations where the forests of a given region switch repeatedly between different states. For instance, in an old-growth forest, ecologically influential treefall events would be rare, because the mature, canopy-forming individuals are long-lived and the mid-storey trees are typically too small to cause consistent disturbance effects (Larson *et al.* 2015). However, when a treefall does occur in such an ecosystem (i.e., after tree death or major disturbance), the magnitude and cascading after-effects of the event can be profound. Another case is forests in which stand-replacing events occur, such as after a rare but intense wildfire or catastrophic storm. This can lead to a persistent unimodal size distribution of trees, with common ages (Muir 1993). In such a situation, large individual treefalls might not constitute an important component of the system for decades or centuries; perhaps never, if the return interval of the disturbance is sufficiently frequent. Yet even in these cases, the process of succession might lead to multiple peaks in the frequency distribution of treefalls, derived first from the shortest-lived, fastest growing colonist species, and eventually as a result of the stochastic deaths within the climax community of canopy trees.

Conclusion

Systematically incorporating dynamic components of a forest like treefall (dead wood) as legacy components into forest-plot measurements and studies of forest processes should encourage researchers to consider and apply more active and standardised approaches to exploring the ways in which patterns link to underlying processes. For instance, snap-shot observations of living trees in forest plots are collected largely because they are thought to capture the realisation of a suite of ecological and evolutionary processes (Aakala *et al.* 2007). Forests should thus be envisaged as not just a static landscape type, but as a complex system that can be theorised, observed, experimented and modelled in a consistent way. This sentiment was echoed centuries ago by the French explorer, Bruni D'Entrecasteaux, who upon seeing the majestic tall forests of Tasmania wrote: *"nature in all her vigour, and yet in a state of decay seems to offer to the imagination something more picturesque and more imposing than the sight of this same nature bedecked by the hand of civilised man."* (Duyker and Duyker 2006). The science of forest ecology ought to capture the vigour of these systems that so impressed D'Entrecasteaux, and this begins by progressing and enhancing our understanding of forests, both vital (living) and decaying (dead), into more of an integrative framework.

CHAPTER VI

READING THE FOREST LOGBOOK: ENVIRONMENTAL DRIVERS OF LIVING AND DEAD ELEMENTS OF AUSTRALIAN EUCALYPT FORESTS

The dead elements of a forest (fallen logs, standing dead trees, coarse woody debris) play an active role in shaping forest structure and dynamics (e.g., decomposition, structural complexity, mortality). However, testing the quantitative relationships between the living and dead trees is challenging because of the confounding role of climate feedbacks. We addressed this issue by investigating the ecological dynamics of tall eucalypt forests in permanent plots across Australia, with particular focus on six located in Tasmania and six in Western Australia. We collected data on the number, location and size of dead and living trees and used generalized linear modelling to identify the best predictors of these attributes. For the most common species across all Australian plots we explored the relationship between number of

trees (and fallen logs) per size class and the carbon stored (as volume). Western Australia had consistently lower density of living and dead elements across the 12 plots, and there was no relationship between the number and biomass of these attributes. Tasmania by contrast, had a strong positive relationship between the density of trees for both the living and dead components, but not between the living and dead biomass. These results highlight the importance of understanding the interrelationships between climate and disturbance and their influence on the structure and function of two contrasting regions within the tall eucalypt forest biome of Australia.

Introduction

Forests are a major global biome, stocking up to 80% of the planet's terrestrial surface carbon and absorbing, in the past decades, about 30% of annual anthropogenic CO_2 emissions (Dixon *et al.* 1994, Pan *et al.* 2011). Projected pressures due to global changes, including expansion of agriculture and biofuels, forestry and climate-driven shifts, pose significant threats to global forest biodiversity, structure and function (Pimm and Raven 2000, Newbold *et al.* 2015). Understanding how these pressures and threats manifest and interact across the landscape is critical, particularly for the conservation and management of these ecosystems (Oliver and Morecroft 2014). Forests span across wide biogeographic and climatic ranges, which ultimately create the diversity of forest-types that we see today. Despite the recognized role of climate in shaping forest distribution and structure at macro-ecological scales, other environmental factors such as disturbance (e.g., fire, windthrow), plant-plant

interactions (e.g., competition), and feedbacks among these drivers can also play a key role (Ulanova 2000, Bowman *et al.* 2015). Separating the effects of climate from such drivers is a key challenge in studies of forest ecology.

Establishing permanent plots in similar forest-types and across broad environmental gradients is a common method used by ecologists to examine the influence of climatic variables (such as mean annual precipitation and mean annual temperature) on the structure and composition of forests (e.g., Bongers *et al.* 1999, Pyke *et al.* 2001, Ter Steege *et al.* 2003). Researchers can use 'snap-shot' patterns of individual trees from measurements of their spatial positions, to recover information of past processes; building an 'ecological archive' of the forest community (Wiegand *et al.* 2003). Detailed information obtained using this approach is often based on the attributes of the living trees. However, it is often the dead elements (logs, standing dead trees and coarse woody debris CWD) that can act as an open book to past climate and disturbance history, persisting on the forest floor for hundreds of years (Harmon *et al.* 1986). The fallen/dead wood as a crucial dynamic component of a forest is increasingly receiving recognition in scientific literature (e.g., Harmon *et al.* 1986, Jonsson 2000, Buettel *et al.* 2017, Buettel et al., in press). Such information can not only improve our knowledge of a forest's past and comprehension of its present, but also our capacity to predict – and possibly manage – its future.

One of the challenges associated with 'reading' the dead components of a forest is to isolate the effects of different variables. For example, some forest types, such as the Mediterranean temperate forests or Amazonian rain forests, are associated with specific climates (Thompson *et al.* 2009), which makes disentangling the relative

importance of climatic factors and disturbances a nontrivial task. In this framework, useful insights can be provided by the study of Australian eucalypt forests. This vegetation type spans a wide latitude range and with a variety of biogeographic regions and climatic settings, from tropical to seasonal-Mediterranean to cool temperate (Ashton and Attiwill 1994). Despite their wide range, eucalypt forests – also known as sclerophyll forests – are all characterized by the presence of dominant species belonging to the genus *Eucalyptus*. Recent studies have started examining these forests on a continental scale, providing useful data to gain a better understanding of their ecological drivers. Between 2012 and 2015, for instance, Wood *et al*. (2015) established a series of permanent plots (AusPlots) located in eucalypt forests across their entire Australian bio-geographic and climatic range, to investigate the macro-ecological drivers of their distribution. However, little to no information was collected on the dead part of the forest, with no data on the number, biomass, and position of logs and CWD.

In this paper, we couple ecological dynamics of the living and dead, to gain a better understanding of the influence they exert on each other. We expand on the work of Wood *et al*. (2015), by adding information on logs and CWD for 12 AusPlots, located in Tasmania and Western Australia. These two macro-locations are characterized by strikingly different climates, where Tasmania is on average cold and wet while Western Australia is hotter and drier. By drawing from these data, we aim to remove climate as a confounding factor in the study of forest attributes such as site characteristics, tree size distribution, and biomass and density of the living and dead. Site attributes which are easy to collect in the field can in fact be important predictors of basal area (BA) of both living and dead components of a forest. Data from plot

networks can hence be employed to answer a range of questions, in some instances beyond the original scope for which they were designed. This paper provides examples of the information required to answer these questions, and some of the methodological decisions that need to be made when the variables tested present analytical challenges.

Materials and methods

Data collection

The AusPlots Forest Monitoring Network is comprised of 48, one hectare (100 × 100 m square) permanent plots in the tall eucalypt forests spanning the eastern, southern and western coastal regions of Australia. These plots were established between 2012 and 2015 as part of the Terrestrial Ecosystems Research Network (TERN), that includes measurements of tree height, diameter at breast height (DBH), spatial location of every individual >10cm DBH, species identity, and tree status (alive or dead) (see Wood et al. 2015 for further details on the locations, establishment and characteristics of the 48 plots). In 2016, for 12 of the 48 plots (six in southern Tasmania and six in the southwest of Western Australia), additional measurements of the coarse woody debris (CWD) were added; this included counts of 'small' CWD (<5m length and <20cm DBH), and all 'large' fallen logs (>5m length and >20cm DBH) with spatial location, length, DBH, and direction being recorded. The Tasmanian plots used were: Bird Track (BT), Mount Field (MF), North Styx (SX), Weld River (WD), Warra (WR), Arve/ZigZag (ZZ); the Western Australian plots were: Carey (CA), Collins (CL), Dombakup (DK), Dawson (DW), Mt Frankland (FR), and Sutton (SU) (Wood et al 2015). Slope data, used to create digital terrain surfaces for

each plot, were collected in the field at a resolution of 5m for all 12 plots, as per the method described in Buettel et al. (under review).

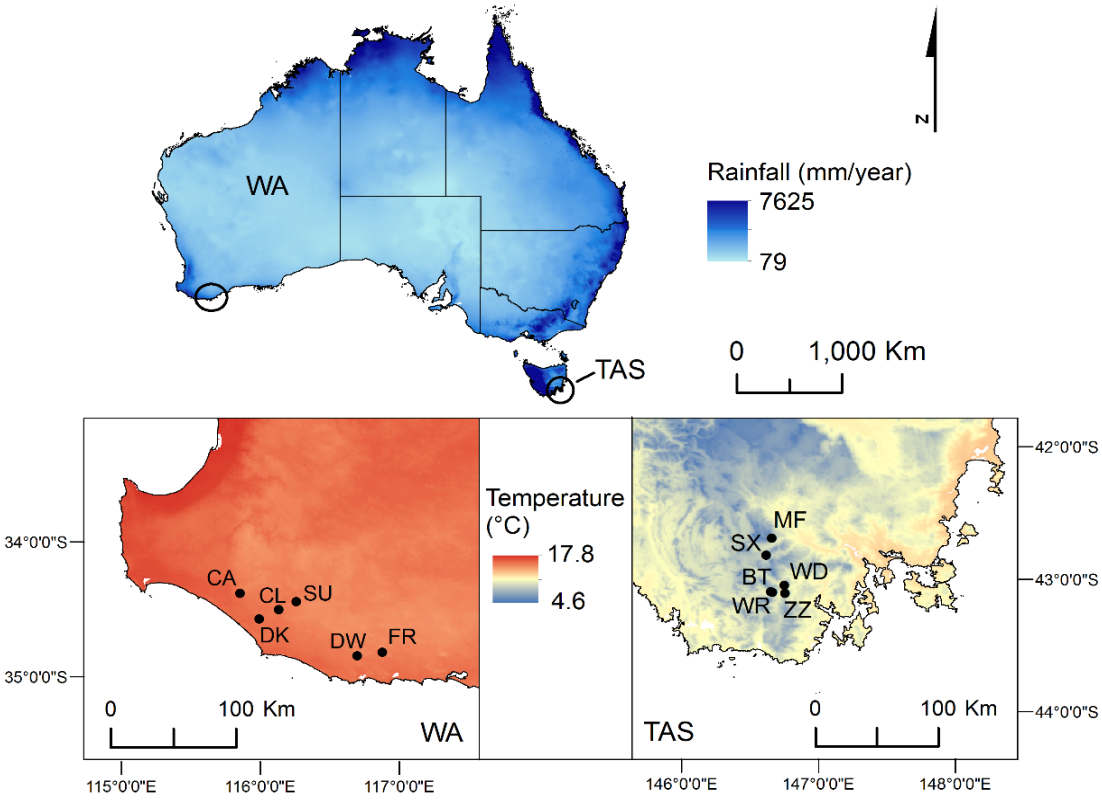


Fig. 1. Location of the 12 Tasmanian and Western Australian AusPlots for which data on number and volume of dead trees was collected. The insects show the exact location of each plot and mean annual temperature values. Mean annual rainfall is displayed in the main map.

Data analysis

The distribution of mass in the trees and logs

Over 20,000 trees were measured across the 48 AusPlots, with a total of 185 species (Wood et al., 2015). For this analysis, we focused on the 12 tree species with > 100 individuals and measurements for height and BA (for statistical robustness). The species that fit this criterion included: *Eucalyptus regnans, E. diversicolour, E. obliqua, E. grandis, E. pilularis, Acacia melanoxylon, Allocasuarina decussata, E. delegatensis, E. delegatensis, E. jacksonii, E. fastigata, Allocasuarina torulosa* and *E. guilfoylei*. Because these plots are in the tall eucalypt forests of Australia, it is no surprise that the species fitting the categories are primarily *Eucalyptus* species. For all species (Table 1), we analysed the frequency distribution of tree volume and hence of carbon mass, calculated using BA and height of the individual trees.

The mass function of each species is based on a histogram of the number of individuals $N(m)$ versus volume by size class. Size classes were defined for each species by dividing the volume range in ten bins, with bin edges starting at volume $v = 0$ and ending at v_{his} (the cumulative volume; Table 1). This relationship was approximated statistically using an exponential function:

$$N(v) = N_o \, e^{\frac{-v}{m_o}}$$

where N_o is a constant set by the total number in the sample, and m_o is a constant with units of volume which sets the slope of the fitted line. For each species, the line of best fit is determined, and the values of m_o are given in the results. The mass distribution function was determined for the fallen logs using data collected from the six

Tasmanian and six Western Australian plots (Fig. 1). Additionally, all logs were analysed collectively, because it was often not possible to identify them to the species level due to decomposition.

Plot level analyses

To evaluate the relationships between the living and the dead components of the tall eucalypt forests, we used the six plots in Tasmania and six in Western Australia (Fig. 1 above) for which we had fallen log data which we could directly compare to the living tree data. Because we were interested in testing the impact of site characteristics independent of climate and biogeography, we excluded all variables that appeared only in one region (for example: *Macrozamia fraseri* – cycads in Western Australia, and *Dicksonia antarctica* – treeferns in Tasmania). To evaluate if dissimilarities between plots in number and biomass of living trees and dead elements (standing dead, logs, and CWD) within and between regions could be ascribed to climatic differences, we calculated the difference between mean annual precipitation (MAP) and mean annual temperature (MAT) across the 12 plots. To assess if the characteristics of dead trees were associated with those of living trees within a given plot, we examined the correlation between number and basal area of living trees and the sum of values for twigs/snags and logs.

To test the factors associated with CWD density and BA of the living trees (BA_{LIVING}), we fitted single-term generalized linear models (GLMs) in Program R v 3.3. Since all fitted models had the same number of parameters, fit could be assessed directly by the percentage of deviance explained (%DE, a scaling of likelihood relative to the null

[intercept-only] model). A Poisson distribution was used to assess the best predictors of CWD count (discrete, positive data) against the following factors: slope (degrees), aspect (cardinal direction), ferns (presence/absence), clumping grass (presence/absence), woody seedlings (presence/absence), bare ground (presence/absence), and shrubs (presence/absence). The Gamma distribution was used for the analysis of BA_{LIVING} with the same factors. For both CWD and BA_{LIVING}, we investigated whether the effects of the two best predictors were likely to be driven by the same underlying ecological mechanism/process, by comparing the sum of the deviance of the two single-term models with the deviance explained by the two-term model that fitted both predictors additively. These data are available in Supplementary Material, Appendix 4.

Results

Plot characteristics

The Tasmanian plots had a consistently higher density of living trees, standing dead, and logs (Figs. 2, 3). The number of living trees per plot ranged from 287–1028 in Tasmania compared to 110–292 in Western Australia. There was a similar pattern for dead trees, ranging from 66–137 per plot in Tasmania and 3–38 in Western Australia; for number of logs it was 50–186 in Tasmania and 39–63 in Western Australia. There was a clear climatic distinction between plots located in the two States. All Tasmanian plots were consistently wetter and cooler than the Western Australian plots (Fig. 4a, b). Tasmanian plots typically had many more living trees per hectare, but not substantially higher living biomass values (Fig. 4a); they did, however, show a greater

number and biomass of dead elements (standing dead and logs) (Fig 4b). There was a linear relationship between number of living trees and number of dead trees (standing dead plus logs) in Tasmanian plots (Fig. 5a), but this relationship was much weaker in Western Australia (Fig. 5b). No clear relationship between the biomass (basal area) of living and dead elements was detected in either Tasmania or Western Australia (Fig. 5c, d).

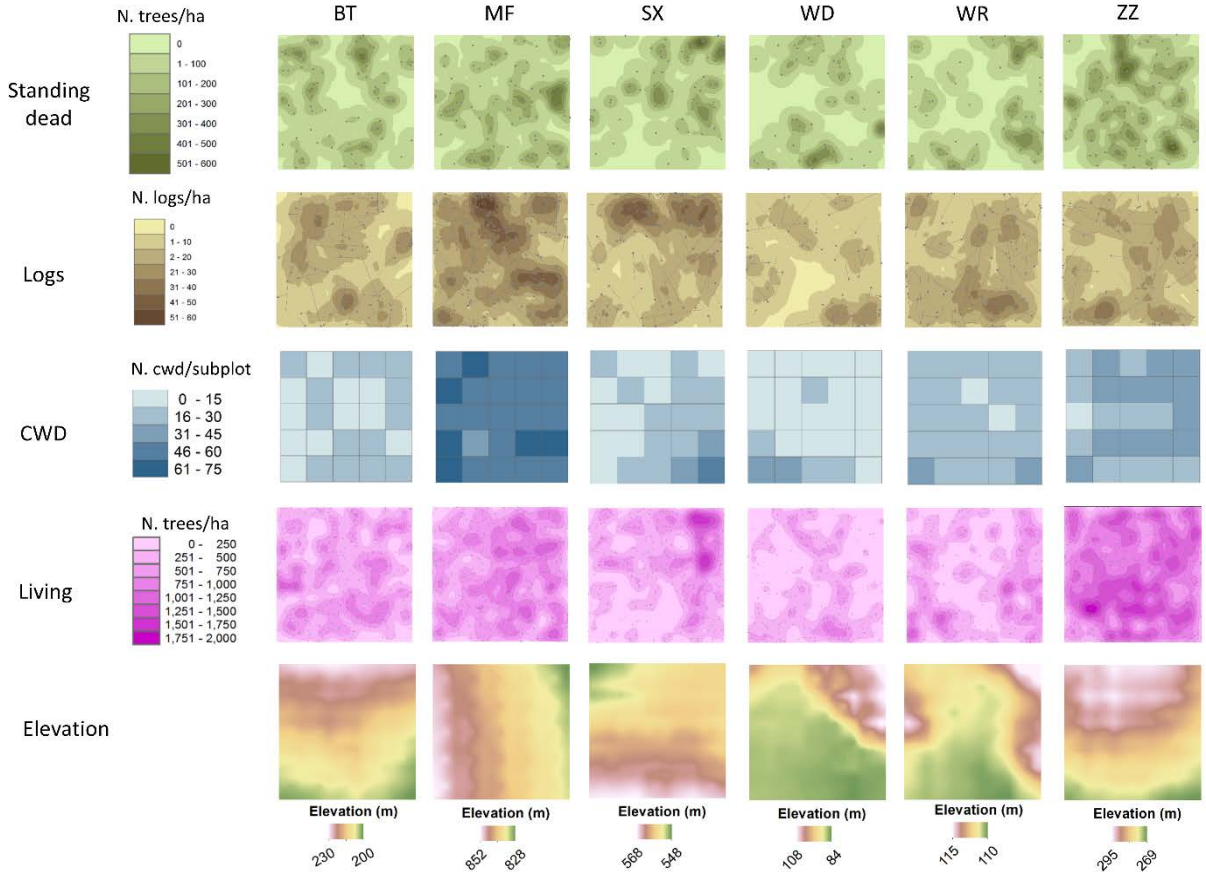


Fig. 2. Heat maps representing density and distribution of standing dead trees, fallen logs, coarse woody debris (CWD), and elevation in the plots located in Tasmania. The density of logs, standing dead, and living elements was consistently high across plots, while CWD showed more variability. In order to display topographic differences, elevation scale varies for each plot.

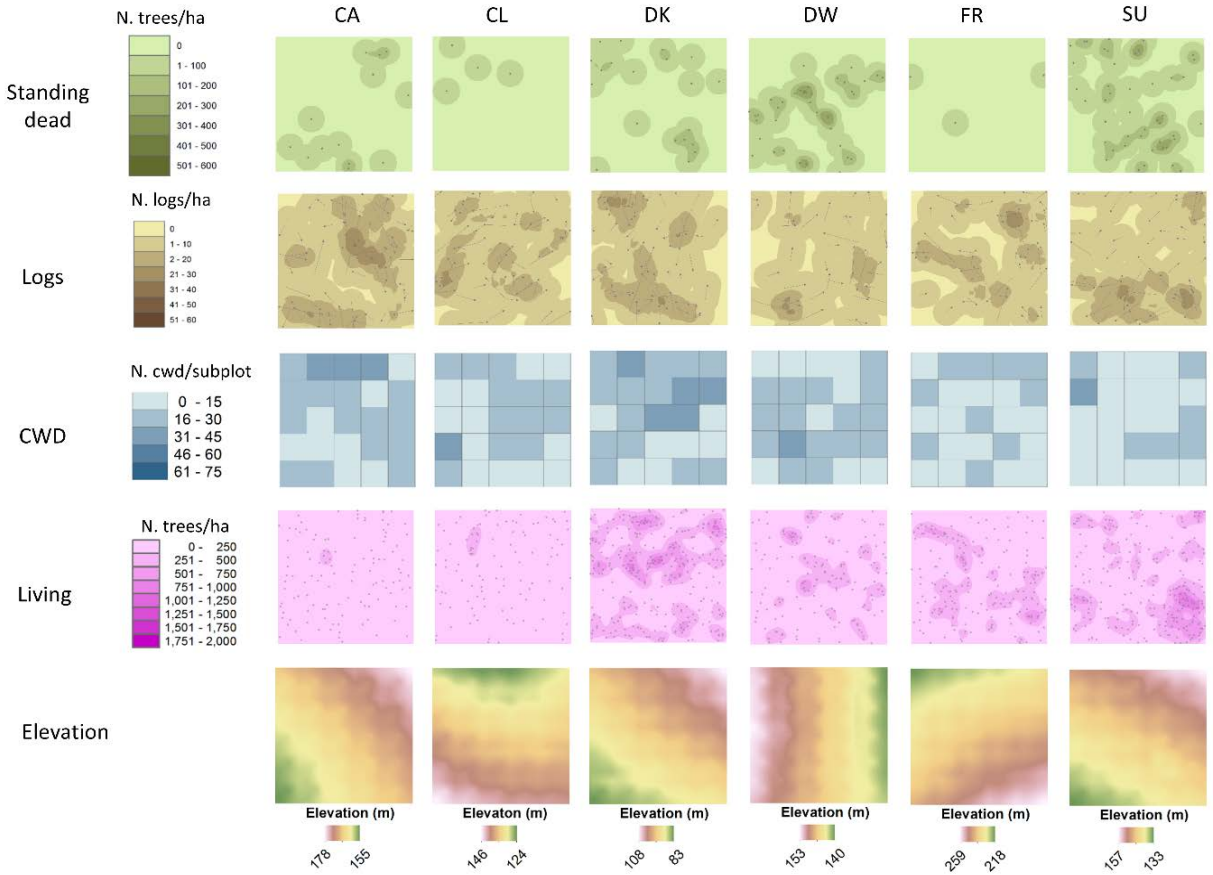
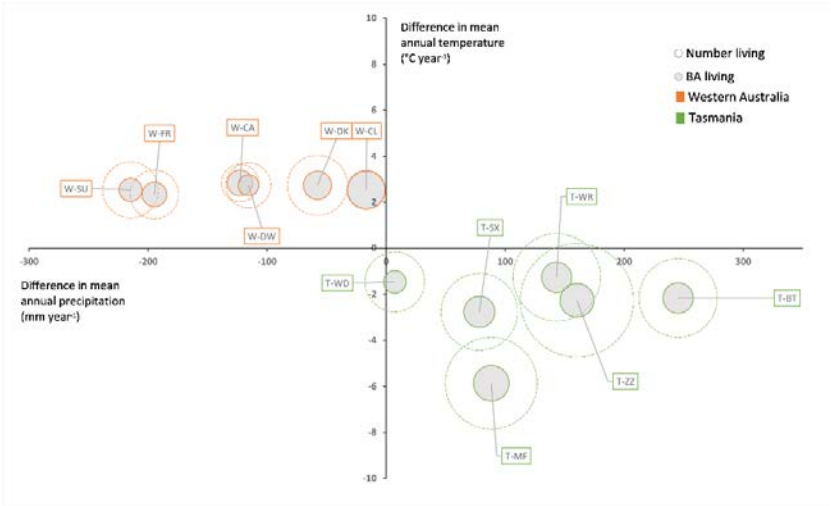


Fig. 3. Heat maps representing density and distribution of standing dead trees, fallen logs, coarse woody debris (CWD), and elevation in the plots located in Western Australia. The density values of logs, standing dead, and living elements were lower than those recorded in Tasmania, with the exception of CWD. In order to display topographic differences, elevation scale varies for each plot.

(a) Living



(b) Dead

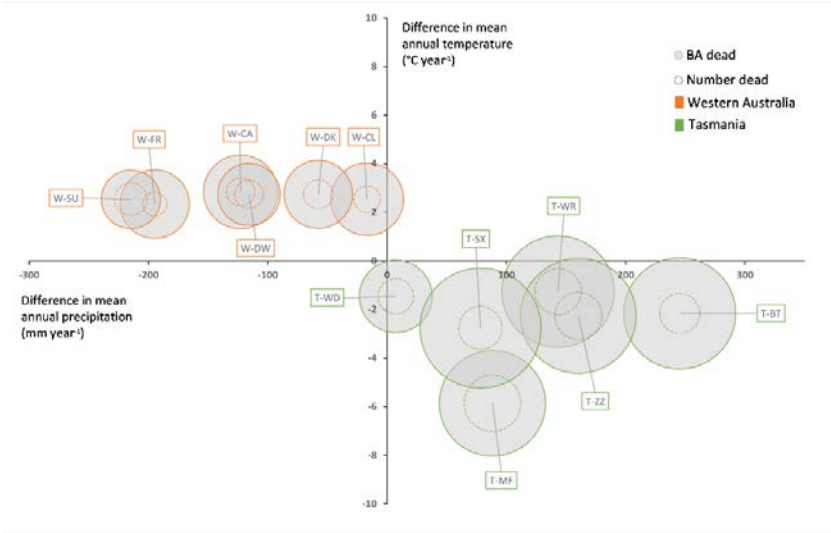


Fig. 4. Number and biomass of (a) living and (b) dead elements, represented based on their deviation from the average mean annual precipitation (x axis) and mean annual temperature (y axis). In all Tasmanian plots, mean annual temperature was lower than the 12-plot average, and mean annual precipitation was higher, while Western Australian plots were characterised by lower mean annual precipitation and higher mean annual temperature.

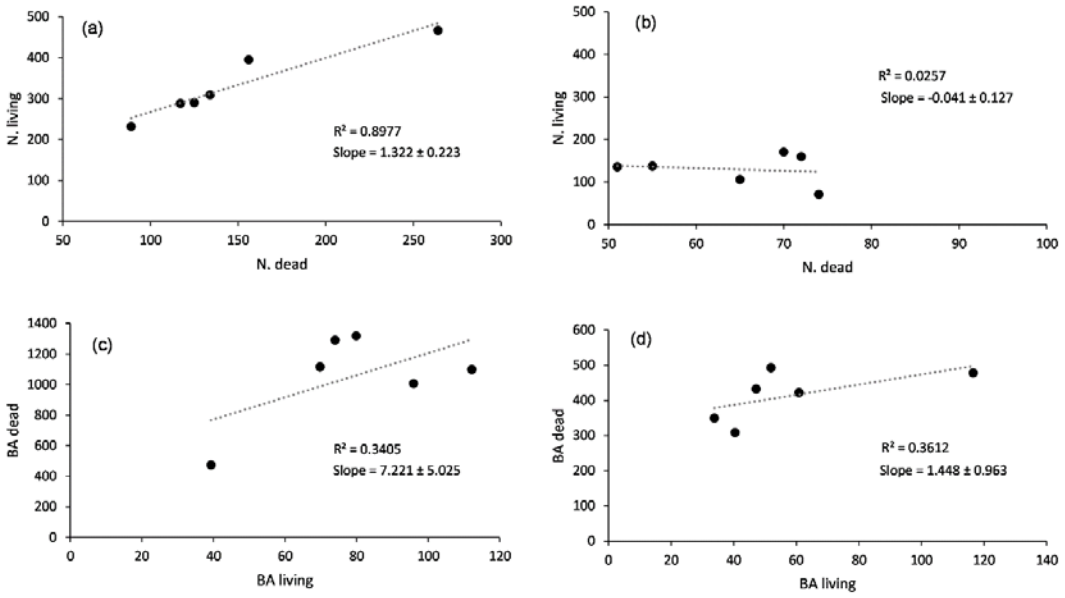


Fig. 5. Relationship between number of living and dead trees in (a) Tasmania and (b) Western Australia and between BA_{LIVING} and BA_{DEAD} in (c) Tasmania and (d) Western Australia. The only strong relationship was between the number of living and dead trees in Tasmania. Trendlines, R^2 values, and slope (± standard error) are indicated.

At a plot-by-plot scale, the quantity of CWD was best explained by the number of woody seedlings and the presence or absence of clumped grass. The number of woody seedlings, which served as a proxy for disturbance or presence of canopy gaps, explained 21.4% of the total deviance, and it was inversely related to the quantity of CWD. The presence of clumped grass—a likely sign of frequent or at least recent disturbance—explained 27.9 %DE and was positivity related to CWD quantity. The model including both predictors explained 55.1% of deviance, which was more than the sum of the single factor models (49.3 %DE), suggesting that the factors woody seedlings and clumped grass influence the quantity of CWD through different (and complementary) mechanisms. The presence of ferns was associated with higher

BA_{LIVING} (22.9 %DE), but the strongest association was with clumped grass cover (56.9 %DE). Unlike CWD, the model including both predictors explained 59.4% of deviance, less than the sum of the single terms (79.7%), likely indicating partial correlation effects.

Species characteristics

The lines of best fit are shown in the figures, and the values of *mo* are given in Table 2. For 10 of the 12 common species, the logarithmic distribution was consistent with a straight line (Fig. 6a-d) irrespective of tree size. Two species, *Eucalyptus delegatensis* and *Eucalyptus jacksonii*, did not fit the exponential distribution model (Fig. 7); both were characterised by a high number of small trees (with some very large individuals in the latter) which might indicate that their numbers are not in equilibrium following a disturbance event. Graphs showing the distribution of each species are presented in Supplementary material, Appendix 4.

Table 2. Total number (*n*), volume (*v*), cumulative volume (*vhis*) and slope (m_o) of the best fit line for the 12 most common species across the 48 AusPlots forest network.

Living tree species	n	*vhis* m^3	$\Sigma\, v$ (m^3)	m_o (m^3)
Eucalyptus regnans	583	180	$1.7 \cdot 10^4$	26
Eucalyptus diversicolor	502	180	$1.3 \cdot 10^4$	37
Eucalyptus obliqua	420	45	$9.3 \cdot 10^3$	20
Eucalyptus grandis	322	35	$3.6 \cdot 10^3$	13
Eucalyptus pilularis	276	180	$8.7 \cdot 10^3$	32
Acacia melanoxylon	254	10	$5.9 \cdot 10^2$	2.6
Allocasuarina decussata	224	10	$5.9 \cdot 10^2$	2.6
Eucalyptus delegatensis	188	20	$2.3 \cdot 10^3$	10.9
Eucalyptus jacksonii	174	200	$7.5 \cdot 10^3$	61
Eucalyptus fastigata	151	45	$2.4 \cdot 10^3$	14
Allocasuarina torulosa	146	4.5	$2.6 \cdot 10^2$	1.8
Eucalyptus guilfoylei	117	6	$4.6 \cdot 10^2$	1.7

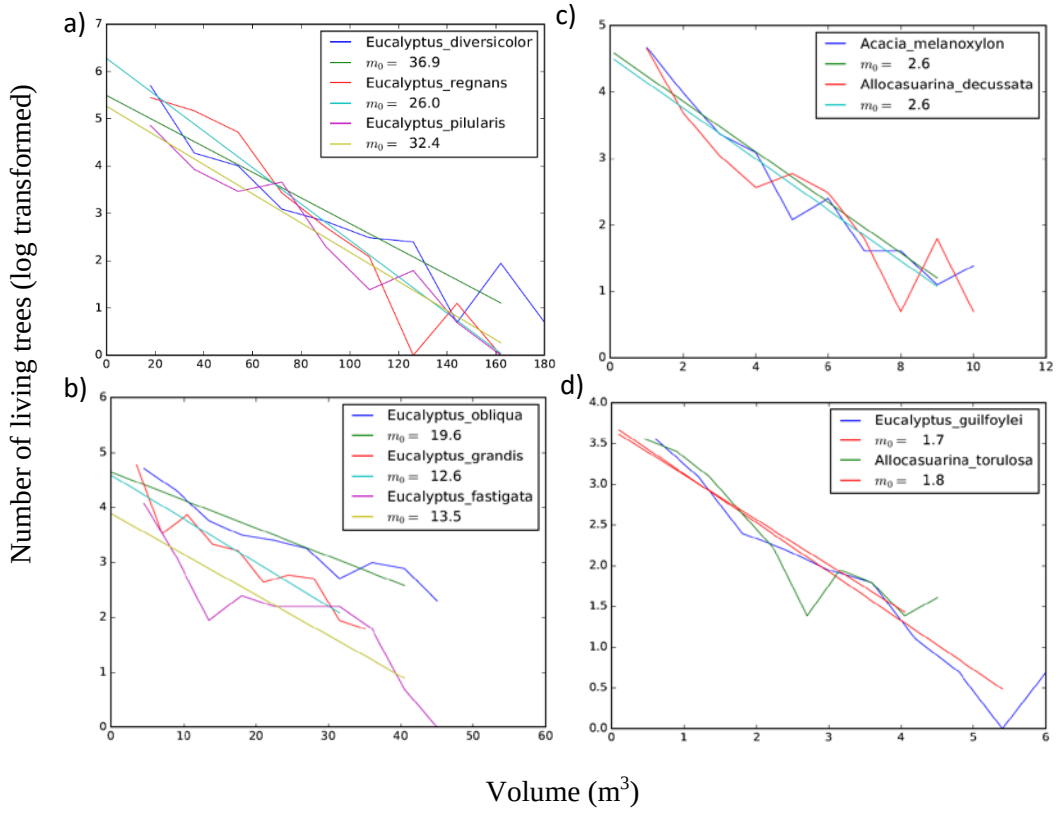


Fig. 6: The number of trees versus volume for a) large trees b) the medium-sized trees, c) the two species of smaller trees and d) the smallest trees. Best fit slopes are shown in the three panels, and the corresponding m_o values are presented in Table 2.

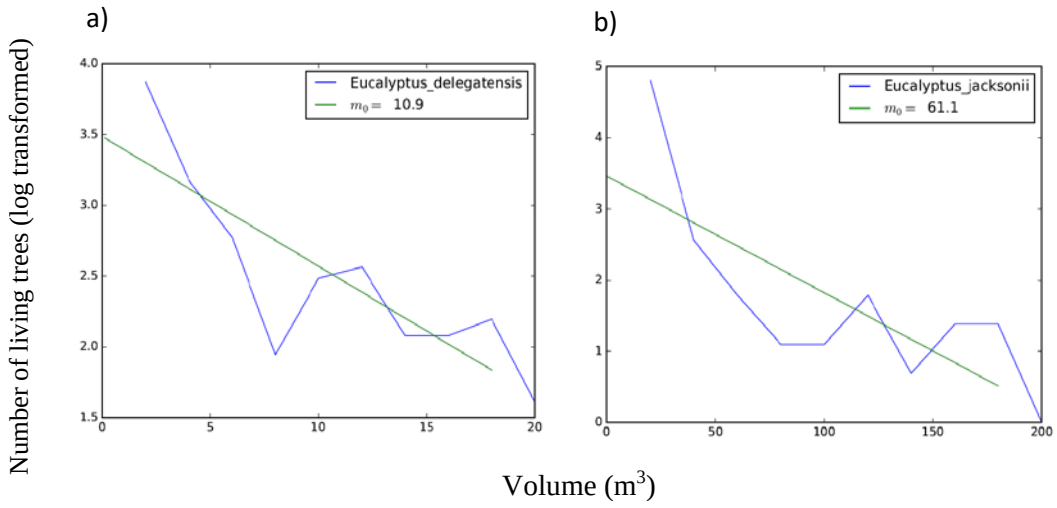


Fig. 7: Relationship between the number of trees and volume for the two 'anomalous' tree species a) *Eucalyptus delegatensis* and b) *Eucalyptus jacksonii*.

The distribution of volume of the fallen logs was examined using two fitted functions: an exponential and a second order polynomial (Fig. 7). The fit of the second-order polynomial – which corresponds to an inverse Gaussian distribution for $N(v)$ because the coefficient of the square term is positive – is only slightly better than the linear fit (i.e., exponential function) (Fig.8). The value of m_o for the fallen logs is 6.6m^3 which is in the range of values for the smaller species in Fig. 6c. Since the logs are not classified by species, this value and the data on Fig. 8 represent averages overall. The closest match to the histogram of log sizes is *E. delegatensis*, with a volume of 10.9m^3.

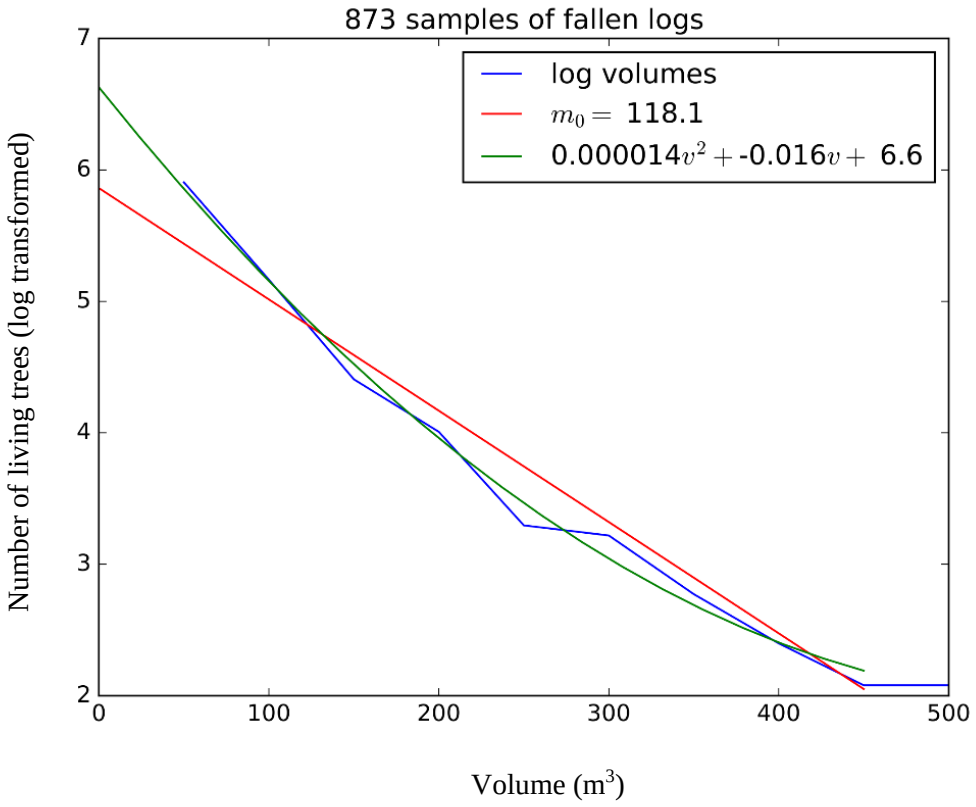


Fig. 8. The relationship between the volume of the fallen logs and the number for all fallen logs in the six Tasmanian and six Western Australian plots. Note: these values represent the average across all 12 plots (not identifiable at the species-level).

Discussion

The geographic and climatic separation between the two habitats (cool temperate in Tasmania, seasonal-Mediterranean in Western Australia) resulted in strong differences in number and basal area of living trees as well as all dead (logs, standing dead, CWD). This was regardless of our choice to focus on a single forest type, the tall eucalypt forest: supporting the role of climate in driving differences and interactions between the living and dead across broad macro-gradients. The survival of the living can be affected by extreme events (e.g., drought) as well as less pronounced but constant changes (e.g., warming temperatures) (Allen *et al.* 2010). The persistence of the dead can also be influenced by climatic changes, as warmer and wetter climates accelerate decomposition (Zhou *et al.* 2007). However, structural similarities and differences between the two climatic bioregions suggest that climate is not the only driver of forest structure and other factors are likely to be involved.

Certain forest characteristics, such as the relationship between the number of trees per size class and the volume of carbon stored, did not vary between regions or across the most common species. The few species that deviated from an exponential distribution were located in different climatic bioregions (e.g. *E. delegatensis* in the cool temperate region and *E. jacksonii* in the seasonal region) and found in fewer plots (Supplementary material, Appendix 4). This suggests that local events such as disturbance also have a key role in influencing volume/number relationship for those species. Furthermore, easy to measure site-characteristics, like the presence or absence of cutting grass and woody seedlings, can give potential insights on how the living and dead components are responding to disturbance (in the same forest type) irrespective of climate and location. For example, of the characteristics that were measured in the

12 AusPlots, the presence of clumped grass was highly correlated with more CWD and higher BA_{LIVING}. This could be indicative of local scale disturbance (i.e., low intensity wildfire) facilitating an increase in the number of small trees (if the basal area is contained in the small trees; no change in the large trees), and thus an increment in the number of standing dead and fallen CWD. The interplay between climate and different types and severity of disturbance in both regions is also likely to be important, as suggested by the strong relationship between the number of living and dead trees measured in Tasmania but not in Western Australia.

For most of Australian vegetation, fire is a key driving force (Gill *et al.* 1981). Deciphering its effects on forest structure in both the short- and long-term is thus essential for understanding the interplay between the living-dead across different bioclimatic zones (i.e., Tasmania and Western Australia). Local fire characteristics are likely to increase even further their influence on vegetation in the future, as climatic changes are likely to alter patterns of fire activity, exposing to more frequent fires some communities such as temperate forests (Bradstock 2010). Indeed, the frequency of wildfires occurring across Australia already risen by 40% over the past few years (Dutta *et al.* 2016Dutta *et al.* 2016). It is likely that the underlying processes determining differences in BA and tree density found in our study could be ascribed to the presence of highly disturbance-driven systems. For instance, Western Australia is subject to higher fire frequency compared with Tasmania (Australia State of the Environment (SoE) 2016, at http://soe.terria.io) and this could explain the lower amount of dead forest elements found in plots located in that region. More research is necessary on the interplay between climate and disturbance, both pivotal drivers of structure and function of tall eucalypt forests. As the climate warms, understanding

how the synergies between these factors could change and how forests may respond is essential for forest management and conservation.

CHAPTER VII

MISSING THE WOOD FOR THE TREES? NEW IDEAS ON DEFINING FORESTS AND FOREST DEGRADATION

The forest ecology literature is rife with debate about how to: (i) define a 'forest' and distinguish it from similar systems, such as woodlands, savannas, parklands or plantations; (ii) identify transitions from 'forested' to 'non-forested' states and, most challengingly; (iii) quantify intensities of degradation. Here we argue that past attempts to define forests and forest degradation, focusing on attributes of living trees (e.g., height, canopy cover), combined with regenerating processes such as recruitment and succession, whilst useful, are ecologically incomplete. These approaches do not adequately represent processes that, operating over long time scales, determine whether a forest system is structurally healthy (as opposed to degraded), functional and persistent. We support our case using a conceptual model to illustrate how deeper-time processes, as well as instantaneous or chronic disturbances that cause degradation, might be revealed through analysis of the

patterns of size structure and density of the fallen wood, in relation to the living trees and standing dead. We propose practical ways in which researchers can incorporate dynamic, long-term processes into definitions of forests and forest degradation, using measurements of dead and fallen trees. Doing so will improve our ability to manage and monitor forest health under global change.

Introduction

The forest biome provides vital global ecosystem services like nutrient cycling and carbon storage, and is the habitat for an immense diversity of terrestrial species (Gentry 1992). Forests also deliver important economic benefits through commercial forestry and tourism, and economic disservices through fire-risk management. As threats to global biodiversity from land-use and other anthropogenic influences such as climate change mount, the future of the world's forests has become progressively more uncertain. As a consequence, many studies focussing on the impact and sustainability of activities associated with human development on forest biomes (e.g. logging and cultivation), and their interaction with the agents of global change (e.g. climatic shifts, altered fire regimes and invasion of non-native species) have been done over the last two decades (e.g. Clark et al. 2011; Lindenmayer and Franklin 2002; Noss 1999). Such studies typically use plot-based surveys as 'snap shots' of standing pattern, time series of marked individuals, and remote-sensed imagery. Such information can then be used to characterise the ecological status of the forest, and to categorise and quantify both forest health and forest degradation over space and time. However, assessing the extent of degradation or loss of forest cover,

and conversely, measuring the success of actions that seek to protect existing forests or ameliorate past damage, remains a fundamental challenge. This is, in part, because the definition of 'forest' and 'forest degradation' is still elusive (Putz and Redford 2010).

Is that a forest, or is that a forest?

There are many different forest types worldwide, some cosmopolitan (e.g. boreal coniferous forests across Eurasia and North America) and others regionally restricted (e.g. mixed Nothofagaceae/Podocarpaceae forests in New Zealand). The forest biome is often sub-categorized according to variation in the structure and dynamics— covering a wide span of climatic and latitudinal gradients. These cross-continental differences make it quixotic to define a generic 'forest' (Chazdon *et al.* 2016). Indeed, the meaning of the term 'forest' can strongly depend on who is doing the defining (e.g., politicians, environmentalists, scientists), and the underlying motivations or concerns for both the forest and the landscape (e.g., maintenance and restoration of ecosystem services, biodiversity conservation, economic gain, land control, recreation and ecological research) (Lund 2002; Perz 2007).

In the era of international conventions and other efforts to enhance forested-landscape restoration and recovery from human-induced impacts, new targeted definitions and concepts of forests are required to help resource managers and academics navigate the complex mosaics that are modern forest landscapes. A scientific working definition '*…land with tree crown cover of >10 per cent, area of >0.5 ha, and a minimum height of 5 metres at maturity*' has been adopted and is used by the United Nations Food and Agriculture Organization (www.fao.org/forestry). Yet a direct interpretation of this

definition also captures a variety of anthropogenic landscapes, such as parklands or monoculture plantations. From an ecological standpoint, it is desirable to demarcate 'natural' systems, and to exclude certain wooded ecosystems that are underpinned by different forest processes and/or are dominated by distinct biophysical features such as grazing or fire (e.g. savanna and/or woodland compared to a boreal forest). But how?

Of planets and streetlights

It is helpful to acknowledge at this point that the problem of vague definitions in science is not isolated to forest ecology. To illustrate, see Box 1 for a classic example. The analogy here with classifying or excluding a land unit as a forest is obvious. What the FAO and similar definitions of forest lack is the equivalent of the planetary 'clearing the orbit' clause (Box 1) – it is missing a *dynamic* component that captures both the ecological vibrancy and time-dependent nature of a functioning forest ecosystem. This is partially a pragmatic choice, because, such events are difficult to measure in remote-sensed imagery or field surveys. Philosophically, this is a poor excuse: it is the ecological equivalent of the 'streetlight effect' (the old joke of searching for dropped keys in an illuminated street where it is easy to see, despite dropping them in a nearby dark alley). We argue that including dynamic elements in the definition of forest (such as the presence of treefalls and associated logs and coarse-woody debris), would not only contribute to a better description of what a forest is or is not, but also could provide valuable diagnostic tools to assess forest health.

Box 1: A classic example if definitional vagueness in science

Consider a well-known recent example in astronomy, where arguments raged on what constituted a 'real' planet, rather than some other solar-system object. In this case, a majority of planetary scientists felt that with the burgeoning number of large Kuiper-belt objects being discovered, the concept of a planet risked being diluted to meaninglessness (Brown 2010). This led the International Astronomical Union (www.iau.org) to formulate a more precise (and arguably scientific) definition of a planet, which included reference to physical dimensions (e.g. a body with sufficient mass for gravity to form a spheroid) and dynamical outcomes (e.g. large enough to have cleared the neighbourhood around its orbit). While not free from some controversial outcomes (most famously, the demotion of Pluto to dwarf-planet status), this new definition excluded many 'unwanted' icy objects and captured all of the 'traditional' rocky worlds and the gas giants. A more scientific, testable and 'future-proofed' concept of what it means to be a 'planet' was established.

Dead wood is key to forest dynamics

Treefall and its consequences (e.g. decaying logs, coarse woody debris, canopy gaps, mortality) are a characteristic marker of turnover in forests, illustrating that even forests considered to be 'in equilibrium' are not just static stands of growing trees, but dynamic ecosystems (Buettel *et al.* 2017). The spatial pattern and physical structure of living, standing-dead and fallen trees can also serve as time capsules, because, they integrate information on past ecological processes, like climatic variation and fire events (e.g. via examination of tree rings, or positions of large fallen logs that create

persistent gaps and leave a legacy of physical displacement on growing trees) (Bassett *et al.* 2015; Swetnam 1993). Yet the presence or consequence of treefall is often not measured in ecological studies, and is not included in contemporary 'operational' definitions of forests; such as the structurally-focused FAO classification based on crown cover and tree height. The measurement of treefalls might also provide a powerful tool for quantifying a forest's carbon stocks (including the living and the dead) and detecting degradation of forested landscapes. The idea here is that alterations in treefall pattern, dynamics and tree mortality (across many different forest types), may be early-warning flags of trends (gains and losses) in forest structure and function (see below).

Reading the forest leaves: what patterns in the coupled living-dead dynamics can reveal

A deforested landscape; one that was once covered with large trees but later converted into agricultural crops, pasture, urban areas, clear fell, or similar is obvious to recognise and uncontroversial to define. However, a degraded forest, as measured against a reference 'pristine' state (which is highly context-specific!), can be far more difficult to quantify. The reasons are twofold:

- The baseline for non-disturbance is contextual and dynamic; are any forests truly in equilibrium or untouched by anthropogenic disturbance (Josefsson *et al.* 2009; van Gemerden *et al.* 2003)?
- There are many possible ways to describe degradation (e.g. tree death, canopy thinning, fire scars) (Ghazoul *et al.* 2015).

To the field ecologist or forester, the earliest stages of degradation are likely to be imperceptible, whereas the final phase will approach a state of degradation where large trees might still remain, but the 'forest' has ceased to support a diverse biota or supply basic ecological services like energy and nutrient flows (Foley *et al.* 2007). For practical and ecological purposes, it is therefore the 'intermediate zone' of degradation, where changes in structure and ecological processes are visibly obvious/detectable, but, the forest is still a functional system that is of most relevance when thinking about forest definitions, management interventions and state transitions.

One obvious feature of the loss of forest health is that the mortality rate of the trees rises. Irrespective of whether this occurs due to direct harvest of the larger trees, a drying trend, disease, or fire, a forest suffering from degradation will usually become more open, with larger and more frequent canopy gaps and fewer living trees. Depending on the nature of the degrading processes, this might lead to a higher proportion of standing dead trees, more logs accumulating on the forest floor, or both. Thus, the interplay between the dynamics of the number and biomass of living trees, standing dead and logs would, as a corollary, provide a *key signature* to the type and rate of the degradation process and recovery rates (Fig. 1). Degradation is not always followed by regeneration. Depending on type, frequency, and duration of disturbance events, forests might cross a critical threshold beyond which they are not capable of regeneration (see Reyer *et al.*, 2015), due to sustained levels of disturbance over time (Fig. 2a), or permanent anthropogenic changes in land use (Fig. 2b). Additionally, these conceptual models (if optimised, and field-verified) could be used for scenario testing and agent-based modelling that would allow for predictions of when forest

health is declining (e.g., mortality is increasing) across both space and time (e.g. by taking a snap-shot survey of a forest to quantify the relative ratio and size structure of living, standing dead and fallen trees). Furthermore, important questions such as "*is the transition from healthy to un-healthy an abrupt threshold?*", "*does degradation occur across a continuum from 'normal' (<10% degraded) to deforested (>90% degraded)?*", "*how can we optimise these conceptual models to detect and predict the early signs of a forest transition passing an abrupt 'tipping point' threshold?*", or "*how many trees can be harvested from a forest stand, and of what size class, whilst avoiding approaching a forest transition that sets the trajectory of declining forest health*" can be conceptualised and then tested using this approach.

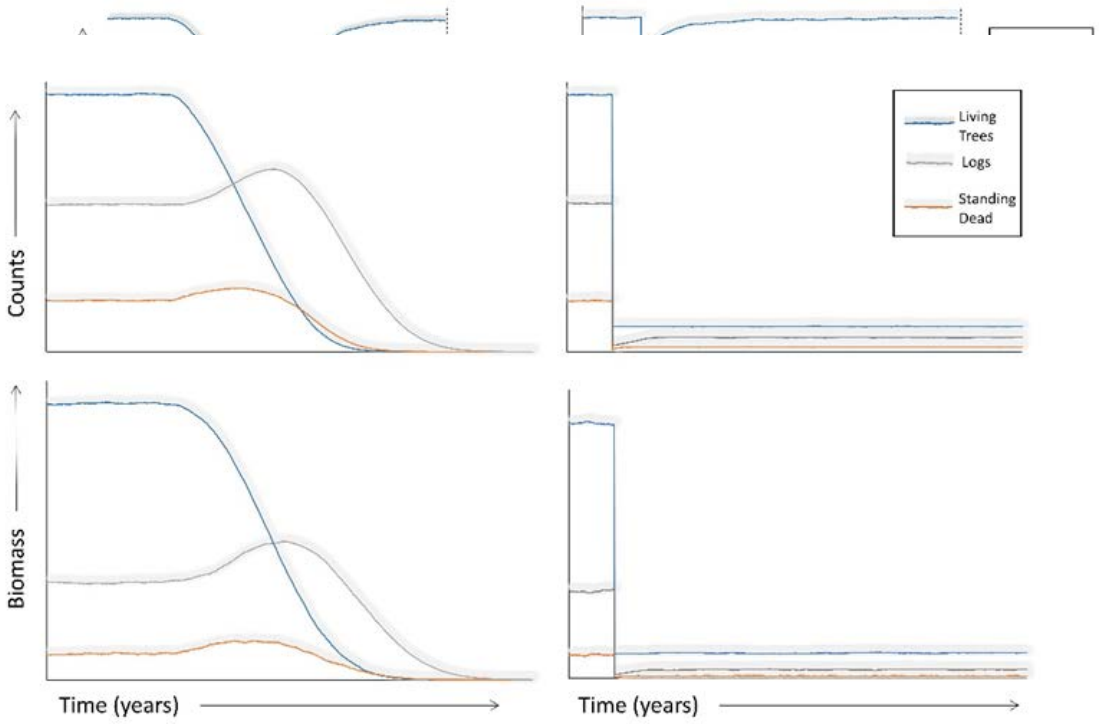


Fig. 1. Conceptual model for a hypothetical forest showing: a) a gradual loss of 50 % of the original biomass, followed by a slow recovery, and b) an instantaneous selective harvest of all large trees, followed by an unfettered period of recovery. In the former case, there is likely to be a period during which living trees are regenerating but the supply of newly fallen logs continues to reduce, leading to a temporary uncoupling of their dynamics (with likely consequences of reduced turnover of nutrients). In the latter situation, the unstable size structure of the post-harvest forest will result in rapid re-establishment of tree abundance, but a slower recovery of biomass, and again, a period of decoupling between the living and dead forest components.

Fig. 2. Conceptual model for a hypothetical forest that: a) degrades systematically over time (e.g., through disease or drying), until the region is completely deforested, and b) experiences a rapid (but not total) deforestation event (e.g., conversion to agriculture), in both cases with no subsequent recovery. In the first case, we would expect to see a lagged rise in the relative proportion of the woody biomass found in standing dead trees and a subsequent lag towards logs—which would peak at some time during the phase of decline of the number and biomass of the living trees. In the latter case, the character of the forest might be quite similar (unless heavily fragmented), but reduced substantially in areal extent.

The key to making use of this information is robust measurement and *calibration*. For example, if baselines of the proportion of living trees, standing dead and logs in 'healthy' forests can be ascertained using comprehensive plot-based data (such as from the Center for Tropical Forest Science, Forest Global Earth Observatory network), then a study of snap-shots of standing pattern in degrading forests would yield valuable insights into the likely nature and extent of degrading and recovery processes (Buettel *et al.* 2017). Ideally, such studies would be coupled with short-term monitoring of the direction of change in accumulation or loss of trees and dead wood components.

Expected proportions of living and dead trees would probably depend strongly on factors like climate, fire frequency, and decay rates. For instance, in warmer, drier

forests, the frequency of fire and activity of termites will typically be high, thereby rapidly removing any lasting legacy of the fallen trees. By contrast, cool-wet rain forests (where ancient logs strewn on the forest floor are among the most persistent feature of the ecosystem), will have a high biomass of dead wood, acting to shape its dynamics over periods much longer than a typical plant lifespan (Vanderwel *et al.* 2006). Such stochasticity in climate and extreme events might make it difficult to determine the 'normal window' of variation in treefall dynamics. In these instances, calibration could be attempted using information 'stored' in the old logs. The age of already fallen trees can be estimated through, for example, the study of the invertebrate and fungal communities they harbour (e.g., Boulanger and Sirois 2007). This also means that past treefall dynamics might be estimated and baseline data collected in a single survey, which would facilitate the application of a modelling and forecasting approach.

In open landscapes like woody savannas, rates and patterns of treefall can often be identified and quantified through remote sensing (Levick and Asner 2013). However, in forests, aerial signs of degradation may disappear within 1-2 years (due to rapid canopy closure and understory re-vegetation), resulting in spectral characteristics not dissimilar from intact forests and consequently poorly distinguishable using conventional space-born remote-sensing techniques (Frolking *et al.* 2009). Forest health may therefore be difficult to assess using current remote-sensing techniques in certain circumstances. However, technological solutions are emerging – for example, downed logs can be mapped using LiDAR in some circumstances (Blanchard *et al.* 2011). Consequently, in the absence of plot networks already established, field-based calibration and regular monitoring of treefall dynamics is a challenging task.

Recent work using more detailed plot information and improved interpretation of remote-sensed imagery has led to substantial revisions in our understanding of forest cover (Bastin *et al*. 2017). However, we argue that the additional benefits arising from monitoring treefall dynamics (i.e. mortality via the frequency distribution of living, standing dead and fallen logs) will provide crucial information that would support forest classification and management. Early detection of deviations from a healthy state, detected through the observation of signs like treefall and dead wood patterns (that might go overlooked if not specifically targeted) would allow managers to intervene before forest resilience is substantially compromised or positive feedbacks kick in (Trumbore *et al.* 2015). For example, extensive logging can increase fire frequency, which in turn further contributes to forest degradation, particularly when combined with drought events such as El Niño-La Niña (Siegert *et al.* 2001). A forest that cannot recover is on a path to becoming something else, given that degradation can alter and potentially interrupt successional trajectories (Ghazoul *et al.* 2015). At its end point, this can trigger a cascade of events affecting the entire local ecosystem, with potential loss of both animal and plant biodiversity (Gardner *et al.* 2009).

Conclusion

We argue that the definition of a forest ought to incorporate *both* attributes of the living trees *and* turnover in the dead-wood component. Together, this combined approach would more effectively characterize an ecosystem that is dynamic. This would allow us to infer whether a tree-covered land unit is likely to be in a static, degrading or unstable state, and potentially vulnerable to tipping into a ‘non-forest’ (Reyer *et al.* 2015). Definitions based simply on living structural features like height and canopy

cover, for instance, *are not* sufficiently ecological because they ignore this crucial dynamism. Recent papers have pointed out that differences in how a forest is defined is due, in large part, to its relevance to a given scientific, economic or social sciences issue (e.g. Chazdon *et al.* 2016). Definitions that reflect a forest's ecological health, by focussing on attributes like regeneration and succession, are vital for identifying degradation (Ghazoul *et al.* 2015). It is time to move away from making suggestions. Instead, we propose that the dead-wood component of a forest should be used to define what a forest is – and is not.

CHAPTER VIII

A PRACTICAL METHOD FOR CREATING A DIGITAL TOPOGRAPHIC SURFACE FOR ECOLOGICAL PLOTS USING GROUND-BASED MEASUREMENTS

Digital elevation models (DEM) are widely used in landscape ecology to link topographic features with biotic and abiotic factors. However, to date, high-resolution, affordable, and easy to process elevation data are not available for many study regions. Here we demonstrate a field-based method for efficiently and inexpensively collecting slope data at a resolution adjustable depending on plot size and research aims. We then describe an algorithm (in the form of an annotated R script) that generates a DEM from these data. To provide an ecological example of the method, we selected four 1-hectare forest plots and compared the DEM generated

by using our field method with those derived from: i) coarse (~30m pixel) data from the Shuttle Radar Topography Mission (SRTM) and ii) high-resolution (~1m) data from Light Detection and Ranging devices (LiDAR). Field- and LiDAR-based DEMs showed strong concordance in two of the four sites. The sites where field-based and LiDAR DEMs substantially differed, suffered from relatively few LiDAR sampling points. Diagnostic tests suggested that the field-LiDAR discrepancy was due to dense over-storey vegetation, which reduced LiDAR's accuracy due to a failure to penetrate the forest canopy adequately in some areas. Our method has the advantage of being quick and cheap to collect yet able to produce small-scale (plot-scale) DEMs of high quality. By using the new R-code we have provided, ecologists will be able to use slope data (collected using any means) to generate a DEM without the need of specific skills in spatial sciences.

Introduction

Digital elevation models (DEMs) are used to represent topographic attributes of the Earth's surface, with a wide variety of practical applications (e.g., in agriculture, engineering, ecology, and telecommunications). They are also indispensable for quantifying environmental threats such as ground instability, erosion and vulnerability of surface features. With improvements in instrumentation, resolution, and the accuracy of remote-sensed data in measuring surface features, DEMs have become ubiquitous in environmental spatial analysis (Ziadat 2007), with particular relevance to the questions of landscape ecology. Technically, a DEM (and the related digital terrain surface) is a numerical data file that embeds information on

topography over a specified area, typically represented by a height map, and is often represented visually as a flattened two-dimensional surface (Hu 1995; Erdogan 2009). DEMs can be generated using many different methods, including photogrammetry, satellite-based imagery, digitisation of existing topographic maps, and field surveying. Each method has its advantages and caveats, and since many scientific studies and applications rely on DEMs, the consideration of data-acquisition costs, quality and accuracy, is crucial.

Many studies have examined factors that influence the quality-feasibility trade-off of DEM construction. Erdogan (2009) proposed three general classes, based on: a) accuracy, density and distribution of the source data; b) the interpolation process (i.e., algorithms); and c) characteristics of the generated surface (represented as uncertainty) (see also Fisher and Tate 2006). Two important influences on the accuracy of the source data of a DEM are sampling density and collection technique. Generally, the most accurate DEMs are produced with precise, highly sampled terrain data (Gong *et al.* 2000; Liu *et al.* 2007). In situations where terrain is complex and/or measured at a coarse resolution, the discrepancy between the DEM and the 'real-world' can be high (Gao 1997; Warren *et al.* 2004). Field surveying methods can yield high-resolution terrain data, but can be time consuming and labour intensive to collect. Alternatively, satellite- or aircraft-based techniques (e.g., Light Detection and Ranging: LiDAR) offer higher-density data capture, but are often limited in availability, expensive to purchase, and can suffer from occlusion of the ground-surface signal in vegetated areas such as forests (Su and Bork 2006).

In landscape ecology, DEMs are most often used to explore the relationship between slope/elevation and various biotic or abiotic variables. These might include forest structure and spatial patterns of individuals or species, fire severity and its behaviour, water and nutrient fluxes, soil properties and solar radiation (e.g., Yin and Wang 1999; Lassueur *et al.* 2006; Seibert *et al.* 2007; Linn *et al.* 2010). Many databases now exist for which slope data are available for mapping terrain at coarse scales (e.g., the Shuttle Radar Topography Mission [SRTM) global DEM), with an effective resolution of approximately 30 metres at the equator; see https://earthexplorer.usgs.gov). This product represents a remarkable achievement in the field of remote sensing, but its resolution might still be too coarse, depending on type and scale of the study. When that is the case, the remaining alternatives are either expensive and require specific skills (e.g., LiDAR), or easy to gather but complex to process (e.g., field data). If you choose to collect your own data in the field, what method do you use to interpolate these measurements? To date, a practical method for developing a DEM statistically, based on open-source software (e.g., Program R, Python), is not available. Such a method would streamline the field data interpolation process and enable field ecologists not familiar with computer software to generate DEMs and DEM plots.

Here we present a simple, practical and accurate method to create a high-resolution DEM, using field-collected slope data. In this short communication, we describe: i) the field-collection method, ii) the analysis algorithm, implemented as an R script, and iii) a working example of how our method compares with two commonly used data sources and methods in the forest ecology literature: the satellite-derived SRTM and local airborne LiDAR.

Materials and methods

Plot design

Slope-angle data was collected from one-hectare plots within the Australia-wide tall-eucalypt AusPlots forest network, laid out on a grid of twenty-five 20 × 20 m subplots (see Wood *et al.* 2015 for details on plot choice, location, establishment and other measurements). For this study, we examined four of the 14 plots located within Tasmania (southern Australia); these were selected because slope information for all three DEM methods: SRTM, LiDAR and field-based, was available. Henceforth these sites are referred to according to their geographic location: "North Styx," "Weld River," "Bird Track," and "Mt. Field".

Slope data collection

The protocol for on-ground measurement of slope was designed to balance accuracy of measurement with time-efficient implementation. Measuring each subplot (marked out by four stake-posts) required two people (hereafter P1 and P2), as indicated in Fig. 1. Slope angles were estimated using a vertex hypsometer; a clinometer would also be suitable. The procedure is described diagrammatically in Fig. 1, for a 20-m subplot. The slopes were measured by P2 by aiming the cross-hair of the vertex towards an eye-height point on P1 and recording the angle (in ±degrees). If dense vegetation obscured the line of sight when standing, both people either crouched or sat (to maintain equivalent level). For 25 subplots, this yielded 100 raw slope measurements.

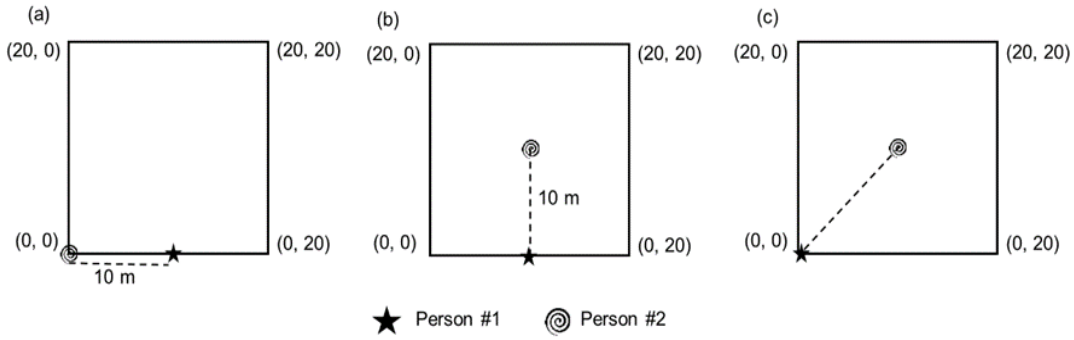


Fig. 1: Methodology to (a-b) determine the centre of the subplot and (c) record slope angle from the centre to each post (post '0, 0' is shown in the example). Measures refer to the extent of the subplots used in the survey (20 × 20 m subplots laid out on a 1 ha grid).

Data analysis – topographic map

Since the dimensions of the subplots were known, the slope heights were calculated via trigonometry (opposite side was based on the observed angle and adjacent side length). Individual subplot heights were converted to a common offset by propagating heights sequentially across each row/column and averaging. The heights of the mid-points of the subplot sides were inferred as the average of the relevant corner post heights measured from adjacent subplots (four values; two for plot edges). Similarly, the centre height was deduced from information on the four corner posts, and the centre-to-corner mid-points as the average height of the two subplot-edge mid-points. This yielded a 9 × 9 raster grid for each subplot.

Once this raster-based digital terrain surface was created, the average or steepest gradients and heterogeneity in heights across the plot were estimated. The raster was

also smoothed (using `image.plots` and `filled.contour` functions in R). It was then converted to a digital elevation model by adding an offset (in metres above sea level) to each point, which is equal to the elevation of the plot derived from a GPS coordinate taken at a known point on the plot and then geo-referenced back to a global DEM such as SRTM.

Sample .CSV data files containing measurements of slopes at four 1-ha plots in Tasmania, are provided in the Supplementary Information, Appendix 5. We also supply commented R code, which can be used to execute all the calculations summarized above. This code will produce raster grids at multiple resolutions, and create digital terrain surface maps and contour plots. The 'field' plot maps shown in Fig. 2 and the Supplementary material are generated with this open-source code, which may be freely distributed and modified (with attribution).

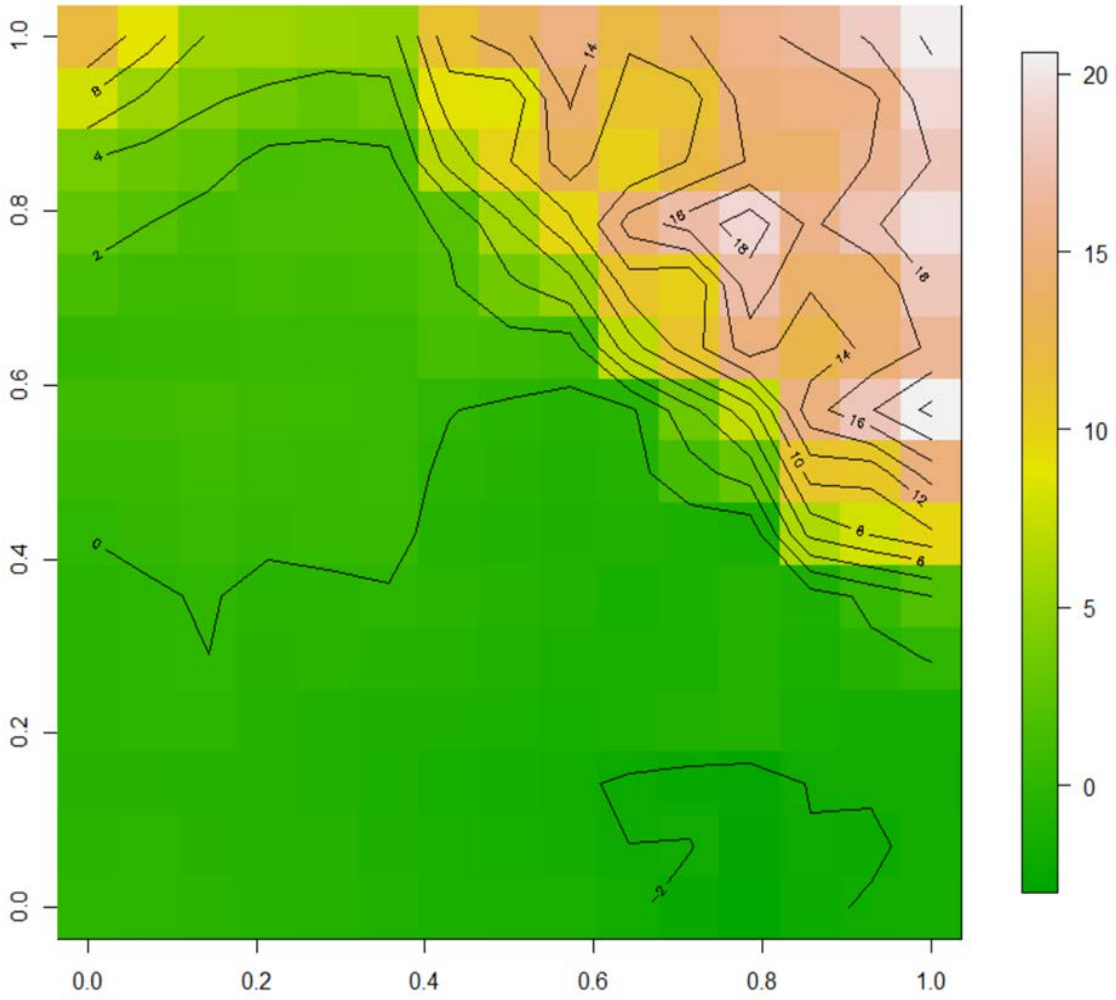


Fig. 2: Example of an R-script-generated raster grid. Contours are imposed using the `image.plot` and `contour` functions of the **`fields`** package. The colours indicate pixel height (in meters), from green (low) to yellow, orange and white (increasing height).

The final DEM for each site was created using the inverse distance-weighted (IDW) interpolation tool in ESRI ArcMap 10.4. These DEMs were compared with models obtained from two alternative sources: 1-arcsecond (~ 30-m) SRTM (provided, for our study region, by Geoscience Australia: http://www.ga.gov.au/elvis), and a 1-m DEM created by triangulating points classified as 'ground' from airborne LiDAR data,

supplied by the Department of Primary Industries, Parks, Water and Environment (DPIPWE) of Tasmania

Statistical analyses

For each of the four study sites, 100 sample points, taken at 10-m intervals were generated (plus a central reference marker). Each of these points were associated to the elevation value extracted from the SRTM, LiDAR and field-based DEMs. Relative elevation was the calculated as the difference in elevation between each sample point and the reference point. We used two methods to compare values derived from alternative DEM sources: i) simple statistical metrics (absolute mean, minimum, and maximum) of differences between pairs of observations (SRTM-LiDAR, SRTM-field method, and LiDAR-field method), and ii) root mean square error (RMSE) for the three pairs of observations.

As a further test of similarity between DEMs, the Pearson correlation coefficient (r) between datasets was assessed, based on the subset of 25 random sample points for each site. This sampling procedure was then repeated (with replacement) 1,000 times to obtain the frequency distribution. All analyses were done using Program R v3.3.3 (R Core Team, 2013).

Results

The number of LiDAR ground points available to generate the DEM varied between sites, with a maximum of 8,014 points for Mt Field and a minimum of 845 points for Weld River (Fig. 3). Graphic representation of ground point density for each site are included in Supplementary Material, Appendix 5 Fig. 2.

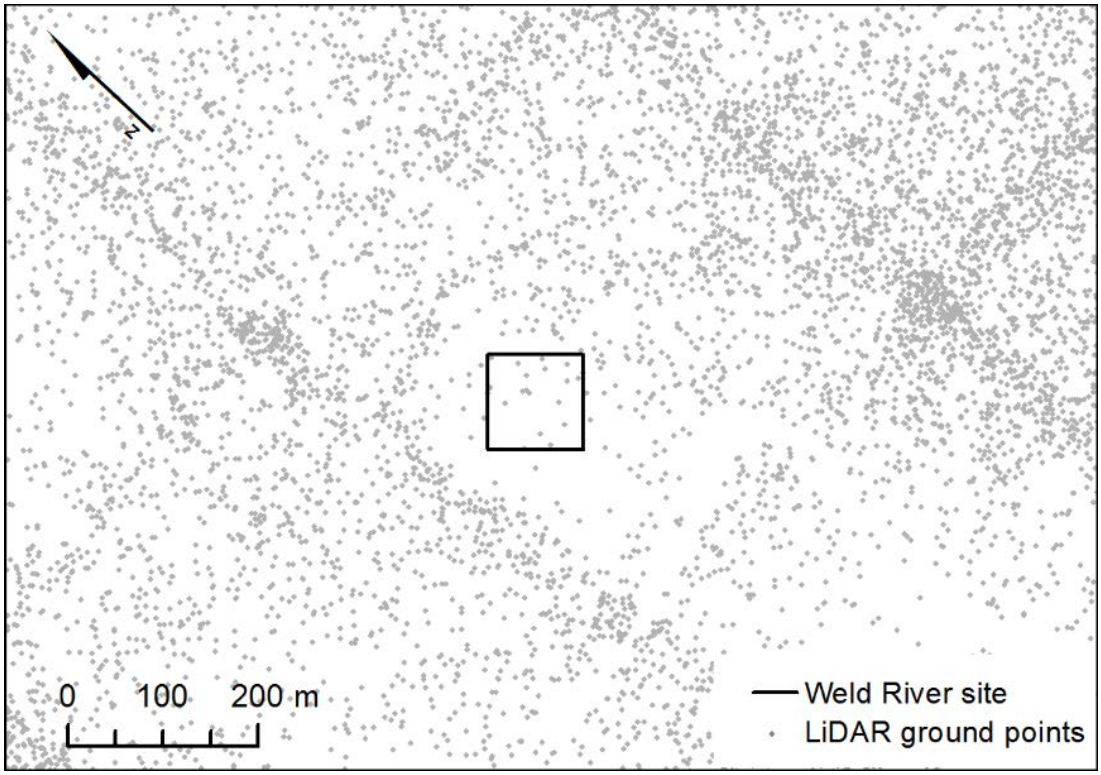


Fig. 3: LiDAR return points classified as 'ground' in the Weld River region, southern Tasmania. The density of ground points in the one-hectare forest plot (square box) is sparse relative to much of the surrounding area, and is the lowest recorded amongst the four sites.

The minimum difference in relative elevation between methods (SRTM, LiDAR, and field-based) was small across all sites, while maximum and mean difference varied greatly depending on the pair of methods compared and the site (Table 1). In the two

sites with the highest LiDAR ground-point density—Mt Field and North Styx—LiDAR and field-based observations were strongly concordant, displaying the lowest minimum and maximum difference, while the SRTM data showed the greatest differences due to its coarse resolution (Table 1; Fig. 4). In Bird Track, all pairs of comparison displayed similar values, whereas in Weld River the LiDAR data differed greatly from both SRTM and field-based data. Consequently, in both Mt Field and North Styx the lowest RMSE values were associated with the comparison between LiDAR and field based data. In Bird Track, by contrast, the SRTM-field method comparison had the lowest RMSE values, while in Weld River this was the case for the SRTM-LiDAR contrast.

Table 1: Summary statistics for the four sites. Minimum, maximum, and mean (± standard error) of the difference (expressed as absolute value) between values obtained from SRTM, LiDAR and the field-based method; Root Mean Square Errors (RMSE) are also presented for each site. Values are expressed in metres. The number of LiDAR ground points available for each site is also reported.

		Bird Track	Mt Field	North Styx	Weld River
SRTM-LiDAR	Min	0.05	0.16	0.08	0.13
	Max	11.81	6.69	16.05	11.99
	Mean ± SE	3.02 (± 0.23)	2.33 (± 0.15)	5.10 (± 0.39)	4.35 (± 0.29)
	RMSE	3.82	2.79	6.39	5.21
SRTM-Field	Min	0.02	0.03	0.03	0.01
	Max	9.96	7.34	14.93	13.23
	Mean ± SE	2.95 (± 0.21)	2.64 (± 0.18)	5.79 (± 0.38)	4.03 (± 0.33)
	RMSE	3.60	3.20	6.90	5.23
LiDAR-Field	Min	0.05	0.03	0.03	0.10
	Max	8.66	3.04	5.42	14.87
	Mean ± SE	3.02 (± 0.22)	0.99 (± 0.07)	1.30 (± 0.10)	6.96 (± 0.35)
	RMSE	3.74	1.23	1.64	7.79
N. of LiDAR ground points		2,527	8,014	4,620	845

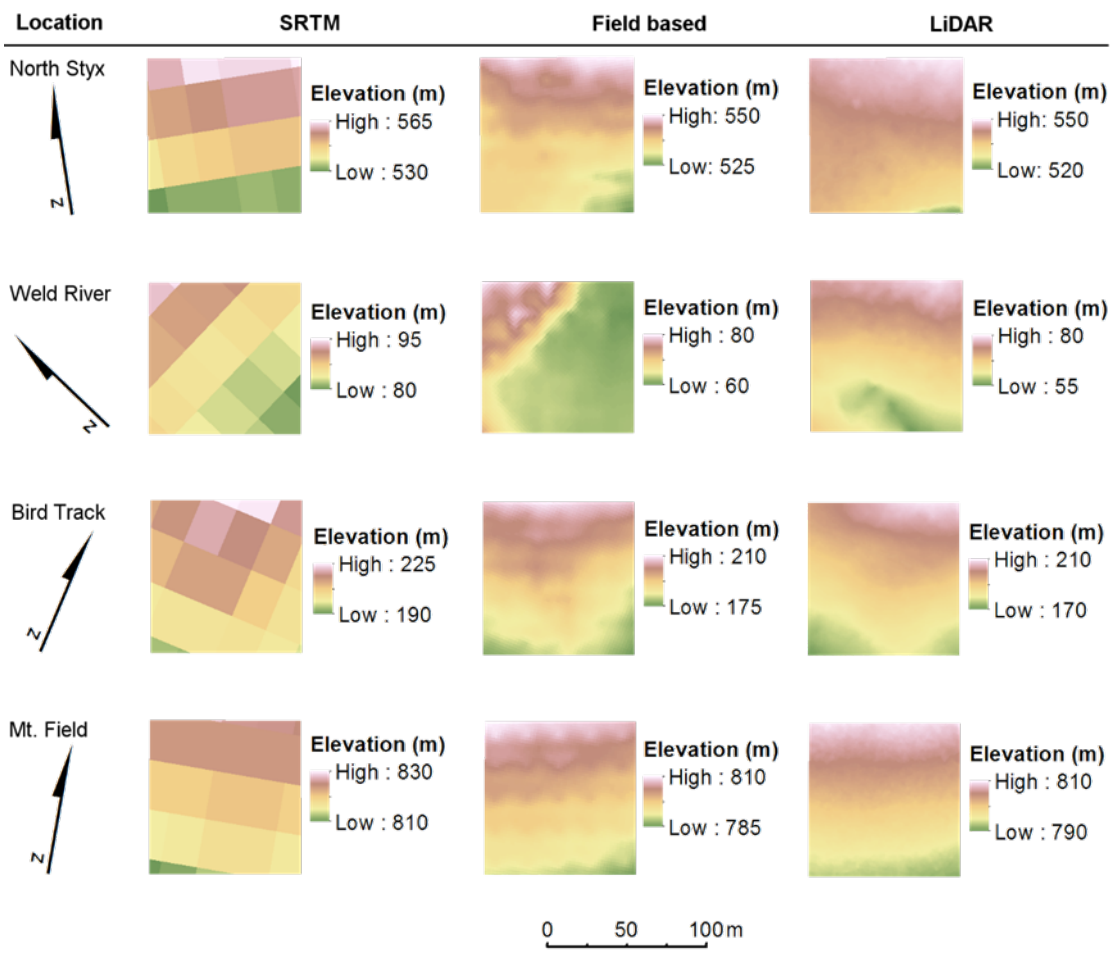


Fig. 4: Two-dimensional contour plots of the digital elevation models of the four surveyed plots, obtained using data from (in order of theoretical increasing resolution): (i) the Shuttle Radar Topography Mission (SRTM), (ii) the new field-based method presented herein, and (iii) LiDAR data.

Analyses of correlation-coefficient distribution agreed with the other statistical summaries. As expected, the relative elevation from LiDAR and SRTM showed only moderate correlation: mean *r* values were between 0.8 and 1.0 in Mt Field and North Styx, while they ranged between 0.7 and 1.0 in Bird Track and between 0.3 and 0.8 in Weld River. The relative elevation derived from our field method were more strongly correlated with LiDAR-derived than SRTM-derived data in all sites but Weld River. When comparing LiDAR with field method, mean *r* values ranged between 0.9 and 1.0 in Mt Field and North Styx (Fig. 5) and between 0.8 and 1.0 in Bird Track. Mean correlation between SRTM and field method was comparatively lower, ranging between 0.7 and 1.0 in Mt Field and North Styx and between 0.8 and 1.0 in Bird Track. In Weld River field observations were loosely correlated with LiDAR data; mean *r* values ranged from 0.0 to 0.8. Conversely, when comparing field method and SRTM, mean *r* values ranged between 0.4 and 1.0. Figures of the frequency distribution of *r* for each pair of comparisons can be found in Supplementary Material, Appendix 5.

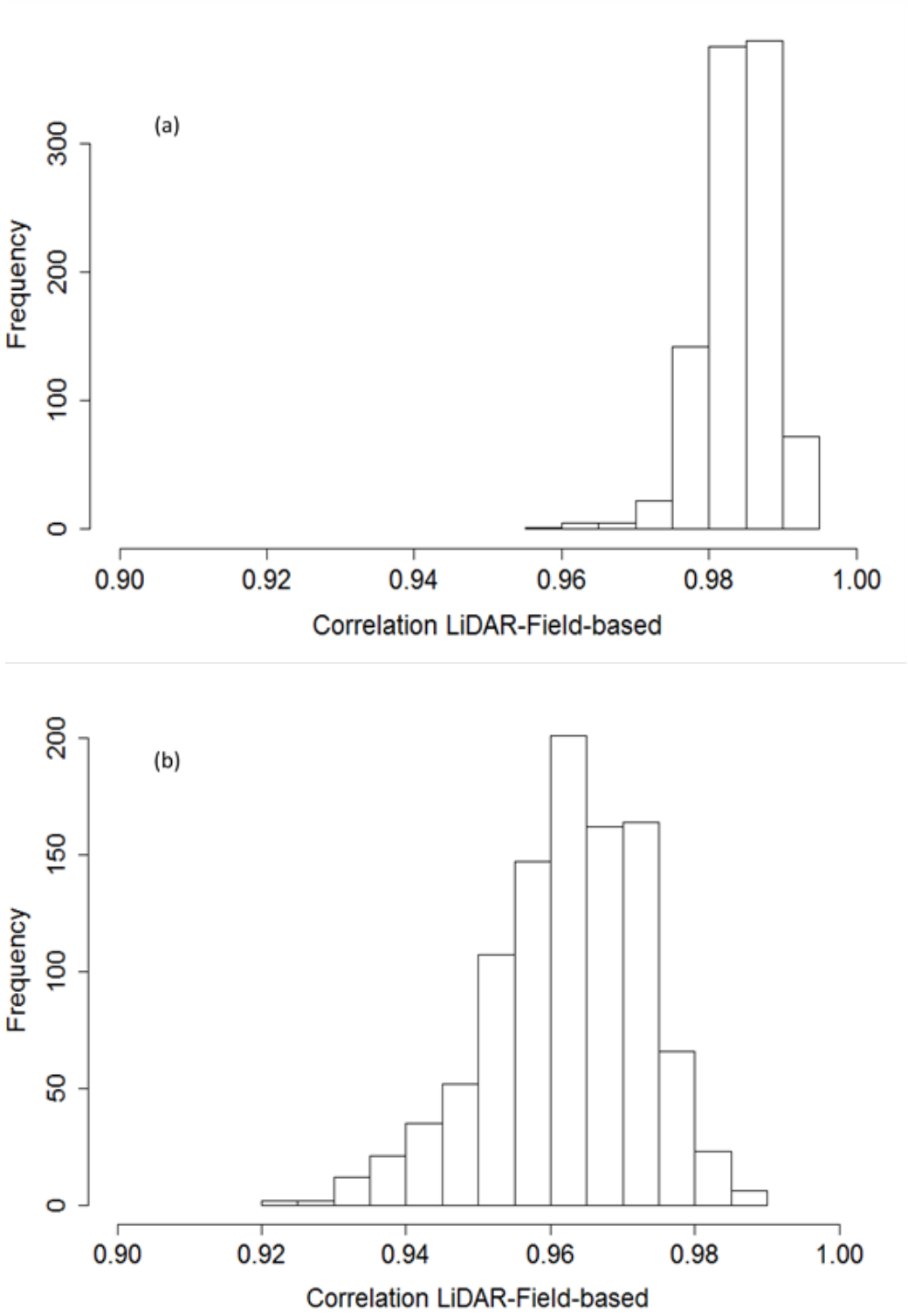


Fig. 5: Frequency distribution of the correlation coefficient between LiDAR and field-based DEM data in (a) Mt Field and (b) North Styx plot sites, displaying consistently high correlation values in both cases.

Interactive 3D renderings of the DEMs generated for each site are in Supplementary Material, Appendix 5, presented as a visual representation of the differences between DEMs obtained using SRTM, LiDAR, and the field-method proposed in this study.

Discussion

We have presented an easy-to-use framework for creation of digital terrain surfaces and DEMs, and outlined how to collect field data in a systematic way to best serve this purpose. In addition, we provide the operational R script and functions for straightforward implementation. This provides a valuable toolkit for field ecologists who seek a means of rapid assessment of landscape features in areas where high-resolution remote-sensed data is unavailable. We demonstrated, using a selection of four 1-hectare forest plots, that the DEMs produced using our method are in strong accordance with those derived from high-quality remote-sensed imagery, and indeed superior in situations of uneven sampling density. Tools for implementation of DEMs into graphical displays, which are simple to interpret and use in subsequent analyses in landscape ecology, are also provided. Such methods can be modified and applied to any DEM derived dataset (irrespective of the data source).

Previous studies have demonstrated that the accuracy of DEMs is strongly influenced by a site's topographic variability and accessibility, as well as methodological issues such as point density, interpolation methods and spatial resolution of raw data (Franklin 2001; Bader and Ruijten 2008; Mitchard *et al.* 2012). Indeed, even once these data are collected there are inherent caveats and challenges when translating this information into a DEM using different frameworks (Guo *et al.* 2010), as summarised

in Table 1. There have been many studies done comparing the use of LiDAR, SRTM and field-based generation of DEMs in ecology (e.g., Schumann *et al.* 2008; Zellweger *et al.* 2014). All point to the conclusion that field-based data collection will, in many practical circumstances, out-perform remote-sensed techniques—most appropriately where sufficient man power and time is available, permitting the modelling of finer topographic variation. The method we have proposed is highly cost-effective and is straightforward to collect and apply, both in terms of field measurements and data processing. By comparison, LiDAR-derived DEMs, whilst powerful, can be expensive to obtain, complex to process with interpolation algorithms, and are not free from error (Erdogan 2009). Further, the generation of DEMs from point-cloud datasets requires specific expertise, particularly when raw data have not been classified on-ground (Liu 2008).

The methods that were used to collect the slope-angle data for the 1-hectare forest plots took two people less than half-a-day per site. Additionally, these on-ground data have high contiguous point density (we used 100 measurements per hectare) and were regularly spaced, resulting in a DEM that is insensitive to the choice of interpolation algorithm (Fig 3; Supplementary Material, Appendix 5). Other advantages of on-ground measurements are that they allow researchers to become intimately familiar with their field sites/ plots (providing a useful 'sanity check' of the final map), and it encourages a standardised protocol. The obvious caveats are the requirement of two people to collect the data, and that in some locations, it can be logistically challenging to access the site of interest (e.g., in complex terrain or remote areas). It is also not suitable for surveying large landscapes, being most cost-effective for mapping small areas, such forest plots in the range of 0.05 to 1 hectare (see Chapter II for a summary

of how common plots of this size are in forest ecology). By contrast, LiDAR and photogrammetric methods can, if resources permit, be readily applied over a wide range of spatial scales while providing good spatial coverage at high resolution with relatively little need for field time (James *et al.* 2006).

The importance of spatial resolution of DEMs is well-studied in landscape ecology, particularly when modelling stream flows (e.g., Dixon and Earls 2009), soil processes (e.g., erosion and runoff) and forest health (e.g., canopy cover, anthropogenic disturbance such as logging; Coops *et al.* 2004; Trumbore *et al.* 2015). Results from such research indicate that the accuracy of slope data, as well as the mean and variance of slope values, decreases with lower DEM resolutions (Chang and Tsai 1991). Most often, slopes estimated from coarse-resolution data (e.g., 90 m pixels) can produce significant underestimates of true slopes (Zhang *et al.* 1999). The results from this study supports these previous conclusions, confirming that higher-resolution methods like LiDAR (~1 m) and field-based (~5 m) approaches out-performed SRTM (~30 m) in all cases except where the LiDAR survey produced an inadequate number of ground points. Given the concordance between LiDAR and field-based DEMs, there is clearly flexibility in the grain at which slope information is collected on-ground (i.e., between ~1-5m), which can be scaled up or down depending on the research question and availability of resources (time and manpower).

Of the four evaluation sites, the LiDAR-derived DEM for Weld River was found to differ substantially from both SRTM and field-based methods (Table 1; Fig 4). This underscores the importance of having a high and consistent density of ground points for generating accurate DEMs. In fact, point density was almost an order of magnitude

lower in Weld than in any other site (i.e., 845 points/hectare for Weld; 8,014 points/hectare for Mt Field), possibly affecting DEM accuracy. The main factor that influences the realised number of ground points generated by a LiDAR survey is the thickness and structure of the vegetation, and the steepness of the slope (Su and Bork 2006). Supporting this inference, it has been shown repeatedly that LiDAR accuracy decreases with increasing topographic relief and canopy density (i.e., fewer ground-points with tall and obscuring over-story; Hodgson and Bresnahan 2004). There were also substantial and systematic differences between SRTM and the other two methods (LiDAR and field-based). This was not only due to the differences in resolution (i.e., SRTM 30m), but also to the intrinsic nature of SRTM imagery. The interferometric synthetic aperture radar (InSAR) used to generate the SRTM data products work by detecting electromagnetic energy in the microwave spectrum (~5.6cm; www.usgs.gov). As radar wavelengths do not penetrate rough surfaces, including the canopy, SRTM products would closely resemble the terrain only on bare ground or grasslands (Farr *et al.* 2007). Although vegetation-corrected SRTM DEMs have been generated, they are based on spatial products ranging in resolution from 3 arc-seconds (~90 m) to 30 arc-seconds (~1 km) (O'Loughlin *et al.* 2016). This does not allow for high-resolution spatial analyses needed for most ecological studies, and is incapable of capturing variations in micro-topography. In our plot-based examples, a major advantage of on-ground methods is that the measurements maintain accuracy irrespective of vegetation type, thickness or number of strata.

Landscape ecology is burgeoning with uses for high-quality DEMs, and there are many potential applications of easy-to-implement methods, such as the one we present here. Some examples of current and future applications for a DEM include: i)

exploring the influence of slope on treefall and forest structure (Buettel *et al.* 2017), ii) microtopography as a link between hydrology, soil stability and species richness/diversity (e.g., Moser *et al.* 2007), and iii) microtopography as a tool to investigate the influence of human and natural disturbances on local forest structure (e.g., Ehrenfeld 1995; Linn *et al.* 2010; Wood *et al.* 2011). There are many innovations involved in the use of DEMs in ecology, and it seems inevitable that ongoing technological advances will reduce costs, improve data quality (James *et al.* 2006), and enhance the role of LiDAR and photogrammetry in the future. For example, 'remote-sensed' (but on-ground) data might become readily crowd sourced (e.g., via smartphone apps), greatly increasing data coverage and reducing costs to the researcher. Furthermore, ground-based methods of collecting high-resolution topographic data are also improving in the form of using robotised total stations (electronic theodolites able to automatically recognise a target, without the need to accurately sight it), differential GPS (improved GPS with accuracy of ~10 cm), and Zebedee, portable hand-held devices equipped with a 3D sensor (James *et al.* 2006; Bosse *et al.* 2012). Indeed, Brasington et al. (2003) reported on their ability to collect up to 3000 observations per day in the field and the technology has since improved. All of these envisaged technological methods may provide a more rapid, precise and accessible alternative to field-based data collection for future research. However, it is unclear when such methods will be widely available, and at what cost. A practical, low-cost method like that presented in this paper can yield a simple, high-resolution alternative that is available now. In making use of easily collectable field-based slope data, it allows for rapid construction of a DEM suitable for tackling a wide range of problems that might confront researchers in landscape ecology.

CHAPTER IX

MODELLING LINEAR SPATIAL FEATURES IN ECOLOGY

The spatial analysis of dimensionless points (e.g., tree locations on a plot map) is common in ecology, for instance using point-process statistics to detect and compare patterns. However, the treatment of one-dimensional linear features (fibre processes) is rarely attempted. Here we appropriate the methods of vector sums and dot products, used regularly in fields like astrophysics, to analyse a data set of mapped linear features (logs) measured in 12 × 1-hectare forest plots. For this demonstrative case study, we ask two deceptively simple questions: do trees tend to fall downhill, and if so, does slope gradient matter? Despite noisy data and many potential confounders, we show clearly that topography (slope direction and steepness) of forest plots does matter to treefall. More generally, these results underscore the value of mathematical methods of physics to problems in the spatial analysis of linear features, and the opportunities that interdisciplinary collaboration provides. This work provides scope for a variety of future ecological analyses of fibre processes in space.

Introduction

Research in forest ecology typically focuses on the structure and spatio-temporal patterns of the living trees. Ecological plot networks, such as the globally distributed Center for Tropical Forest Science (ctfs.si.edu) sites, routinely record data such as the species identity, size and spatial position of trees (Anderson-Teixeira *et al.* 2015). However, the dead trees, enduring as fallen logs on the forest floor, are rarely measured in this way (Buettel *et al.* 2017) other than occasional sampling of the dead wood biomass (Kirby *et al.* 1998) or quantification using remote sensing (Pasher and King 2009; Mücke *et al.* 2013). Yet, coarse-woody debris (CWD) and logs are crucial to the dynamics of forest ecosystems, due to their roles in canopy gap creation, displacement of living trees, cycling of nutrients and organic matter, carbon storage, and provision of habitat for seedlings and animals (Harmon *et al.* 1986). Why then are the spatial patterns of fallen logs, a neglected topic in forest ecology?

One reason for the lack of attention to forest logs may be the logistical challenge of measuring and mapping these complex linear features (McCarthy and Bailey 1994); standing trees can, by contrast, be summarised by a point location and diameter. Another reason is the lack of well-developed quantitative methods for analysing the spatial coordinates of one-dimensional (approximately linear) features superimposed on a two-dimensional grid (Dale and Fortin 2014). The *x*-*y* coordinates of standing trees in a plot are usually analysed as a point-process, treating them as a statistical distribution of dimensionless points in space (Wiegand and Moloney 2013). There has been some success in modifying spatial point-pattern statistics, like Ripley's K, to deal

with ‘fibre processes’ by modelling points distributed regularly or randomly along line segments (Stoyan and Ohser 1982). There are also examples where lines and points have been modelled separately and then tested for interactions, for instance in relation to the location of geological ore deposits along lineaments (Foxall and Baddeley 2002). However, the methodological links between observation of linear features and understanding of the underlying ecological predictors remains nascent. To date, statistical analysis of fallen logs in forests has centred on understanding the frequency distributions of wind throw (Lorrey and Martin 2005), for instance by using ‘rose plots’ to represent number per unit direction (Rouvinen and Kuuluvainen 2001).

How then, might we advance this problem of modelling linear features in spatial ecology? One often-cited approach to achieving methodological innovation is via cross-disciplinary collaboration (Rhoten and Parker 2004), where ‘standard approaches’ from one field are borrowed (or modified) for use in another research area. A well-known example is the adoption of diffusion approximations in ecological dynamics, based on the theory of Brownian motion of suspended particles in a fluid (Lande *et al.* 2003); another is the application of Boltzmann–Gibbs–Shannon entropy, from information theory, to species distributions (Keylock 2005). Here we describe a collaboration between two ecologists (co-authors JCB, BWB) and two astronomers (AC, JD), which sought to address two simple, intuitive, and yet previously untested questions in spatial ecology (Ferry *et al.* 2010): (i) do trees in a forest fall downhill, and (ii) if so, are trees more likely to fall downhill when the slope is steeper? The data are the mapped position and length of fallen logs in 12 one-hectare plots, along with a fine-scale representation of the topographic surface, measured in two regions (the far southern and western margins) of Australia’s tall eucalypt forest system. The problem

of log directionality (linear features) in forests and their potential interaction with a heterogenous surface (slope gradient), is somewhat analogous to subjects in astronomy like inferring gravitational potentials from the projected velocity vectors of clusters of stars (e.g., Brunthaler et al. 2005), or mapping the 3-dimensional distribution of gas and dust near the Sun using polarization of starlight (e.g., Frisch et al. 2012).

Field data collection and spatial mapping methods

Ausplots (ausplots.org) is a recently established network of 48 × one-hectare plots set within the tall-eucalypt forests of Australia. Each forest plot was laid out on a grid of twenty-five 20 × 20 m subplots, with all living and standing dead trees >10 cm diameter at breast height (DBH) identified to the species level, with size recorded and spatial coordinates mapped; see Wood *et al*. (2015) for details on plot choice, location, establishment and other measurements. For this study, we additionally measured fallen trees (logs on the forest floor) in six AusPlots from the far south of Tasmania, and six located in the southwest of Western Australia.

The protocol for on-ground measurement of logs was designed to balance accuracy of measurement with time-efficient implementation. For each plot, the magnetic compass bearing of the four plot edges was recorded. For each subplot, measuring tapes were laid out along the perimeter, and the subplot area was searched systematically in a criss-cross pattern. When a fallen log was encountered, the DBH (taken horizontally, 1.3 m from the base) was measured; only those with DBH > 10 cm and length >5m qualified for mapping. For the mapped logs, the subplot-level *x* and *y* coordinates were determined by drawing a rope towards each perimeter tape; this start position was

recorded from the determined base (uproot or snapping point) of the fallen tree. The compass bearing (angle in degrees) of the log was then taken, and the log length was measured to ±0.1 m. (*Note*: If the base of the tree fall lay outside of the one-hectare plot area, the point of entry was used. Similarly, if the log exited the plot boundary before terminating, its length was measured only through to the exit point.) This was repeated for every subplot, to accumulate a complete tally of fallen trees within each plot, and the same procedure was applied to all 12 studied AusPlots. A total of 873 tree falls were measured, 478 in Tasmania, and 395 in Western Australia.

Using these data, the log direction angles were adjusted to correctly align the field measurements with the plot orientation, to ensure congruency with the maps of the living trees. The subplot-level x and y coordinates were converted to a plot-level $x1,y1$ with the angle and length data used to calculate $x2,y2$ (the endpoint of the logs) via trigonometry. Basal area of each log was estimated by assuming a cylindrical shape for the log; this is a reasonable assumption in this situation, because most large trees in these tall-eucalypt plots have their tops broken off by wind shear prior to falling. Sample .CSV data files containing measurements of bearings and logs at two of the one-ha plots in each of Tasmania and Western Australia, are provided in the Supplementary Information, Appendix 6. We also supply a commented R script (r-project.org), which can be used to do the mapping.

Do trees fall down slope?

Searching for information in the directions of the fallen logs on a plot is essentially a problem of vector analysis. The height and direction (azimuth) of each log gives a vector, and patterns in these vectors can reveal the factors that control treefall. For this case study, we used two methods commonly deployed in the physical sciences: vector sums and dot products (Bielewicz *et al.* 2005). The first approach uses the length of the log as the magnitude (for statistical weighting), while the second sets an equal value to all logs (i.e., having direction, but length equal to one). For the vector sum, the *x*,*y* components of each vector, $\vec{v_i}$ are added,

$$\langle \vec{v} \rangle = \frac{1}{n} \sum_{i=1}^{n} \vec{v_i}$$

and the sum is divided by the number of logs, *n*, as:

This vector sum is compared with its expected value based on the variance of a random walk process:

$$\sigma_v = \langle |v| \rangle \cdot \sqrt{n}$$

where $\langle |v| \rangle$ is the mean magnitude of the vectors in the sample:

$$\langle |v| \rangle = \frac{1}{n} \sum_{i=1}^{n} \sqrt{\left(v_{x,i}^2 + v_{y,i}^2 \right)}$$

If the average vector sum is significantly larger than the random walk value (i.e., $\langle \vec{v} \rangle > \sigma_v$, then there is a favoured direction in the logs, otherwise the distribution is

considered to reflect a chance distribution of directions. Analysis of the unit vectors give a similar result. Using $\hat{u}$ for unit vectors, where $u^2_x+u^2_y = 1$, we then compare the sums: $\sum_{i=1}^{n} \hat{u}$ with $\sigma_u = \sqrt{n}$. If the former is significantly larger than the latter, there is evidence for a coherent pattern in the directions of the logs. This is a simple application of the variance-ratio test for a random walk process (Hunter *et al.* 1993).

Some of the AusPlots show statistically significant alignments of the logs, and others do not. Table 1 gives the two measures of alignment, $\langle \vec{v} \rangle$ and $\sum \hat{u}$, and their magnitudes, divided by the root mean-square (*rms*) error expected from a random walk, i.e. σ_v and σ_u respectively (the two vector sums are displayed on Fig. 1 and 2, in red and blue).

Table 1: Vector sums for logs in 12 one-hectare forest plots from Australia.

plot	n	$\langle \sum \vec{v}_x \rangle$	$\langle \sum \vec{v}_y \rangle$	σ_v	$\lvert \sum \vec{v} \rvert / \sigma_v$	$\sum \vec{u}_x$	$\sum \vec{u}_y$	σ_u	$\lvert \sum \hat{u} \rvert / \sigma_u$
T-BT	64	+2.98	-6.25	2.48	2.79	+11.81	-21.04	8.00	3.02
T-ZZ	70	-3.75	-9.75	2.55	4.10	-10.56	-30.95	8.37	3.91
W-FR	53	-3.53	+5.19	1.65	3.82	-8.70	+20.16	7.28	3.02
T-WD	51	-0.24	-4.44	2.20	2.02	+0.05	-13.48	7.14	1.89
W-CL	63	+3.44	+3.29	1.48	3.21	+17.09	+14.05	7.94	2.79
T-MF	187	+3.45	-0.53	1.00	3.51	+53.04	-3.55	13.67	3.89
W-DW	39	+4.73	+3.86	2.20	2.77	+13.79	+12.43	6.24	2.97
W-DK	60	-0.60	-1.24	1.62	0.85	-5.26	-4.45	7.75	0.89
W-SU	52	-4.38	+1.28	1.89	2.41	-14.38	+2.90	7.21	2.03
T-SX	91	+0.98	-0.28	1.88	0.54	-0.56	+2.63	9.54	0.28
T-WR	82	+0.98	+4.82	2.01	2.45	-1.32	+18.69	9.06	2.07
W-CA	61	-0.47	-0.32	1.95	0.29	-2.88	-0.35	7.81	0.37

This vector-based analysis of the forest logs allows simple comparison with the local topography, by comparing the direction of the vectors $\vec{v_i}$ and $\sum \hat{u}$ with the gradient of the height of the terrain, which has been measured at 225 locations in each of the AusPlots using a Vertex hypsometer. This measured height function, $h(x,y)$ has

gradient $\vec{\nabla}h$. For this computation we interpolate the 225 measured heights using a Gaussian filter (from the Python SciPy ndimage package: scipy.org), and then take the gradient at each of the 10^4 integer (*x*,*y*) grid points. The base of each fallen log is matched to the nearest grid point, and the dot products of the two log vectors, $\vec{v_i}$ and $\hat{u}_i$, with the height gradient, are computed. This gives two sets of scalars, $\vec{v_i} \cdot \vec{\nabla} h(x_i, y_i)$ and $\hat{u_i} \cdot \vec{\nabla} h(x_i, y_i)$, for *i* = 1,...*n*. We then compute the means and standard deviations of each of these two sets of scalars, and test whether the mean is greater than three times the standard error on the mean, $\sigma/\sqrt{n}$. If there were no correlation between the height gradient and the directions of the logs, then we would expect the mean of the samples to exceed three times its standard error only about three times out of a thousand. In fact, as shown on Table 2, the means exceed three times their standard errors for seven of the 12 plots. Note that negative values for the means indicate that the logs are pointing generally downhill, because the gradient operator is defined to point in the direction of maximum increase in height. The height functions, *h*(*x*,*y*), are shown as background colour on Fig. 1 and 2, with the colour bar indicating the values of *h* in metres.

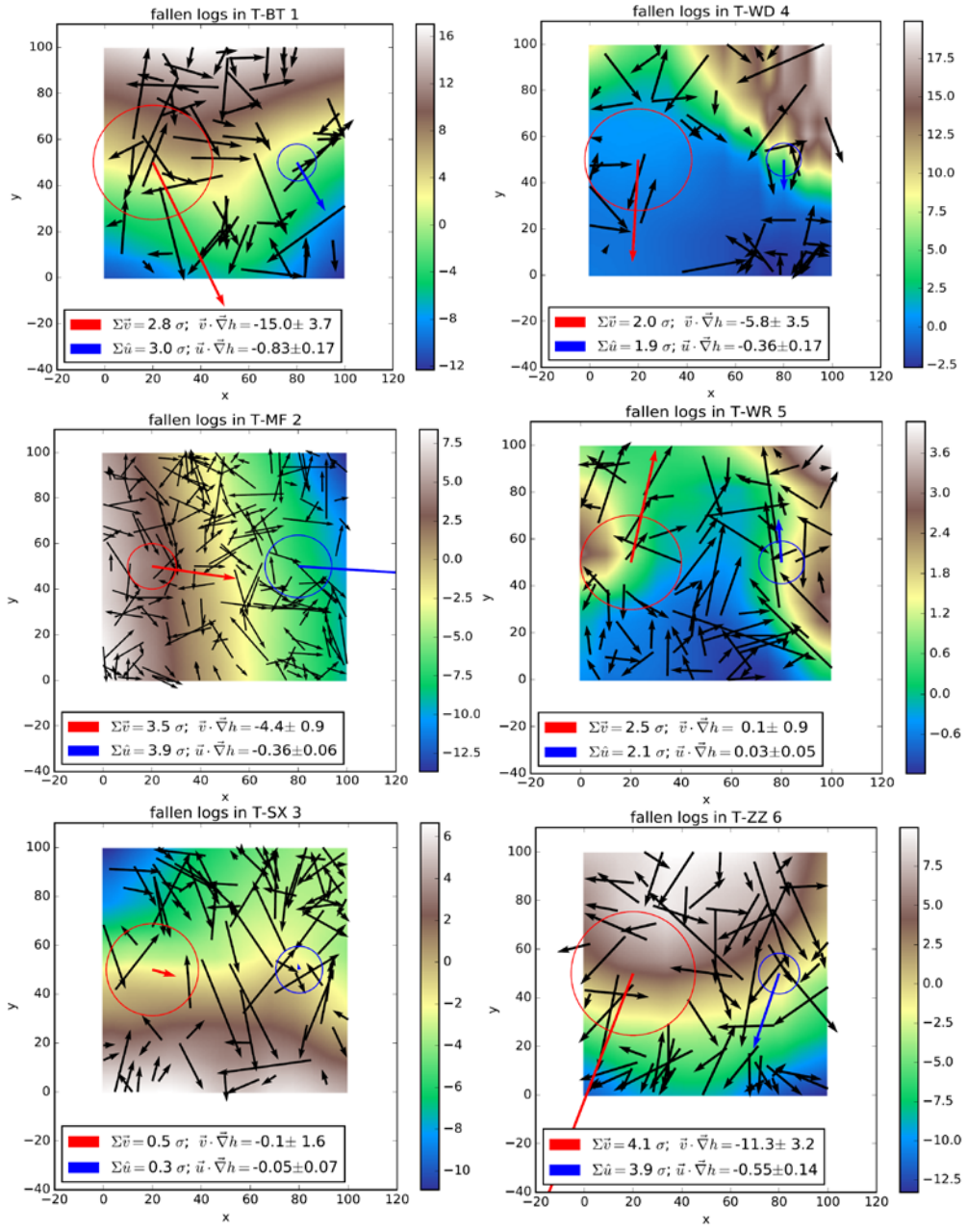


Fig. 1: Six one-hectare plots of tall eucalypt forests in Tasmania, showing site topography (coloured shading, with blue the lowest height grading to brown at the highest), a map of all the fallen logs with diameters at breast height > 10 cm, and results of the analysis of directionality for: (i) the vector sum (red arrow, with circle representing confidence bounds of the random walk expectation) and (ii) dot product (blue arrow and circles).

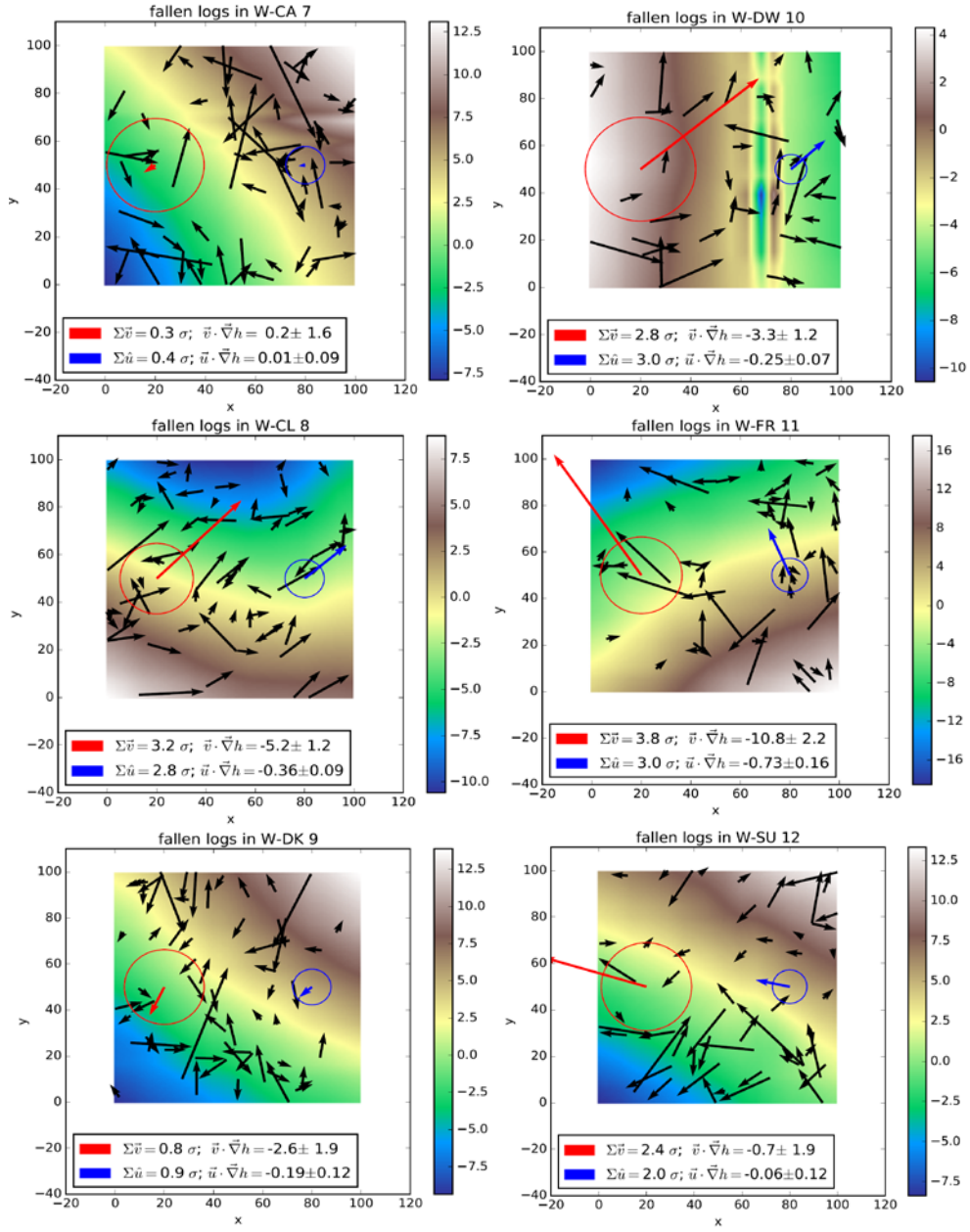


Fig. 2: Six one-hectare plots of tall eucalypt forests in Western Australia, showing site topography (coloured shading, with blue the lowest height grading to brown at the highest), a map of all the fallen logs with diameters at breast height > 10 cm, and results of the analysis of directionality for: (i) the vector sum (red arrow, with circle representing confidence bounds of the random walk expectation) and (ii) dot product (blue arrow and circles).

Table 2: Height gradient dot products, presenting the two measures of alignment and their magnitudes divided by the root mean square error expected from a random walk

plot	n	$\langle \vec{v} \cdot \vec{\nabla} h \rangle$	$\langle \sum_n \hat{u} \cdot \vec{\nabla} h \rangle$
T-BT	64	-14.99 ± 3.68	-0.83 ± 0.17
T-ZZ	70	-11.29 ± 3.24	-0.55 ± 0.14
W-FR	53	-10.81 ± 2.24	-0.73 ± 0.16
T-WD	51	-5.76 ± 3.50	-0.36 ± 0.17
W-CL	63	-5.24 ± 1.16	-0.36 ± 0.09
T-MF	187	-4.44 ± 0.89	-0.36 ± 0.06
W-DW	39	-3.27 ± 1.20	-0.25 ± 0.07
W-DK	60	-2.65 ± 1.85	-0.19 ± 0.12
W-SU	52	-0.68 ± 1.93	-0.06 ± 0.12
T-SX	91	-0.10 ± 1.63	-0.05 ± 0.07
T-WR	82	+0.14 ± 0.86	+0.03 ± 0.05
W-CA	61	+0.16 ± 1.58	+0.01 ± 0.09

Yes they do: but at what gradient?

Given that there is a statistical relationship between the slope of the terrain, $\vec{\nabla} h$, and the direction of the fallen trees in the 12 plots with measured logs, the next step was to assess the dependence of directionality on the magnitude of the slope. For this analysis, we grouped together the logs from all 12 plots as a single set, and compared the mean value $\langle \vec{v_i} \cdot \vec{\nabla} h \rangle$ with $\vec{\nabla} h$, the steepness of the gradient measured at the point corresponding to the base of each log (Fig. 3). Since $\langle \vec{v_i} \cdot \vec{\nabla} h \rangle$ depends linearly on $|\vec{\nabla} h|$, the points on Fig. 3 are distributed in a triangle pattern (the individual logs are plotted as points). Note that the *x* axis is dimensionless, with $|\vec{\nabla} h| * 100$ sometimes called the percent grade. There is a clear downward curvature with increasing *x*.

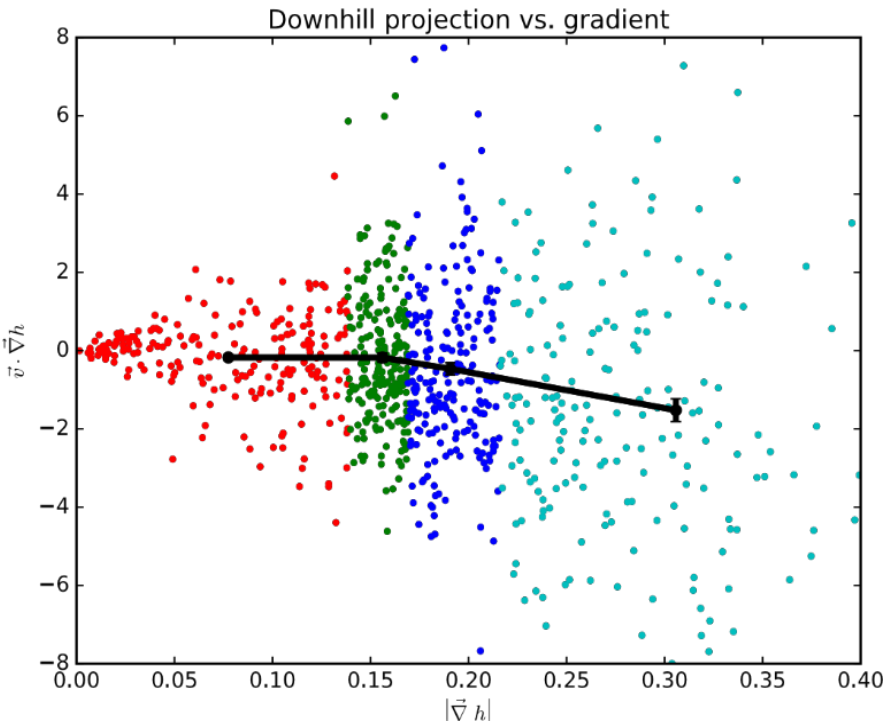


Fig. 3: The vector alignment parameter, $\vec{v} \cdot \vec{\nabla} h$, as a function of slope, $|\vec{\nabla} h|$. The triangular distribution comes from the linear proportionality of *y* on *x*. The *y* scale is in metres, the *x* scale is dimensionless. The black line joins the mean values of *y* for four subsets of the points, with equal quartiles of 208 logs each, as indicated by different colour points.

The v-shape of the distribution of points in Fig. 3 can be removed by dividing by the magnitude of the slope, $|\vec{\nabla} h|$, as shown in Fig. 4. Now the *y* axis becomes:

$$y = \frac{\vec{v} \cdot \vec{\nabla} h}{|\vec{\nabla} h|}$$

(units are metres), such that the magnitude of *y* depends only on $|v|$ (i.e. the length of each log) and the cosine of the angle between the log direction and the uphill direction. In Fig. 4 the points are distributed with roughly constant scatter. To analyse the mean

and variance as functions of *x* we divide the points into quartiles based on the value of *x*, with equal numbers in each, as shown in Table 3. The variance is stable across the quartiles, which is not surprising, since there is no correlation between the slope of the terrain and the length of the logs (Fig. 4). Further, the error bars are not much bigger than the line width, suggesting that we can study the effect in more detail by considering more but smaller sets of points than the four quartiles.

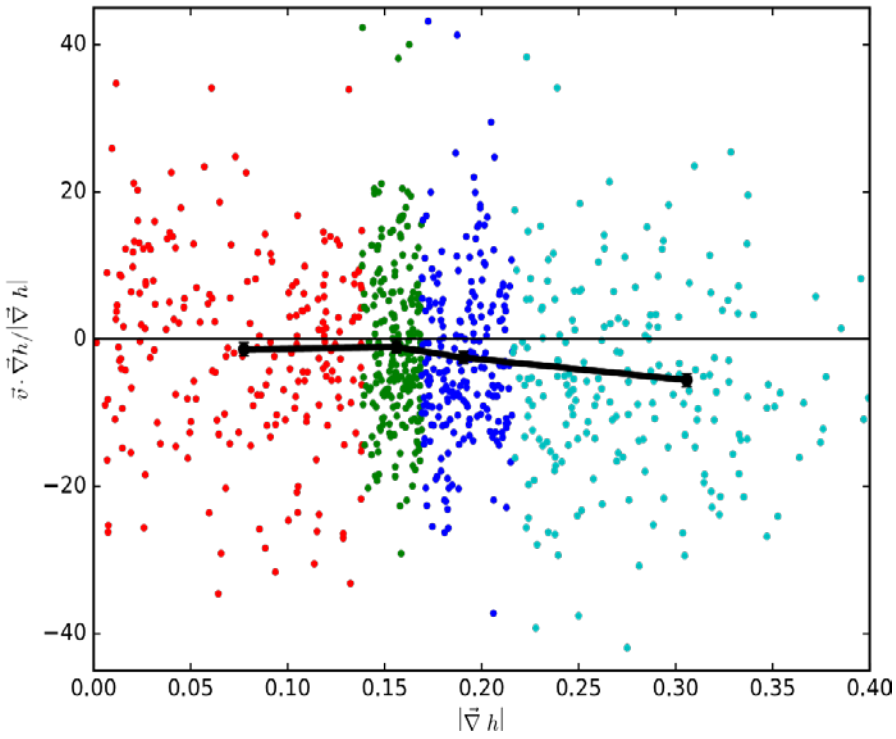


Fig. 4: The vector alignment parameter, $(\vec{v} \cdot \vec{\nabla} h)/|\vec{\nabla} h|$, as a function of slope, $|\vec{\nabla} h|$. The different colours indicate points in the four quartiles analysed in Table 3. Means are marked by black points and error bars, and connected. The heavy black line joins the means, with standard errors also shown. The *x-axis* scale is proportional grade of the slope (larger is steeper), and the *y* axis is in metres.

Table 3: Log direction with respect to height gradient within Australian eucalypt forest plots.

Quadrant	n	median $\lvert\vec{\nabla}h\rvert$	mean $\vec{v}\cdot\vec{\nabla}h/\lvert\vec{\nabla}h\rvert$
Q1 : $0 < \lvert\vec{\nabla}h\rvert < 0.1397$	218	0.079	-1.38 ± 0.90
Q2 : $0.1397 < \lvert\vec{\nabla}h\rvert < 0.1672$	218	0.155	-1.36 ± 0.76
Q3 : $0.1672 < \lvert\vec{\nabla}h\rvert < 0.2065$	218	0.186	-2.74 ± 0.83
Q4 : $0.2065 < \lvert\vec{\nabla}h\rvert$	219	0.277	-5.73 ± 0.86

The mean values of $(\vec{v}\cdot\vec{\nabla}h)/|\vec{\nabla}h|$ in Fig. 4 and in the last column of Table 3. are all negative, meaning that the logs point on average downhill. For all four quartiles of the data, this is a small effect relative to the widths of the distributions (standard deviations are 13.3, 11.3, 12.3 and 12.7 for the four quartiles). However, the large sample of points makes the negative result statistically significant for the two quartiles with the highest values of $|\vec{\nabla}h|$ (right half of Fig. 4, and Q3, Q4 of Table 3. In particular, for Q4, logs on slopes steeper than 20% grade, the mean is -5.73 ±0.86 SE, which is significant at the six-sigma level (Table 3). It is also interesting that the means become increasingly more negative for slopes steeper than 17% grade, which is the median of the sample.

Looking in more detail at the trend in the points on Fig. 4 relative to the plot slope, we divide the sample into 15 equally sampled subsets (n = 58 logs per point), rather than just four quartiles. The result is shown on Fig. 5. The points on Fig. 5 are crowded together for the x-axis range $0.15 < |\vec{\nabla}h| < 0.20$ because the measured logs are most frequently observed on slopes in this range (see green and blue points on Fig. 4). Absolutely flat ground is rare on any of the AusPlots. For slopes less than about 3% ($|\vec{\nabla}h| < 0.03$) the logs actually point uphill, but only at about one sigma significance or

less; as such, this result is statistically indistinguishable from a random expectation at this gradient. The best linear fit (y = 1.877 + (x * (-26.87)) is indicated by the dashed line.

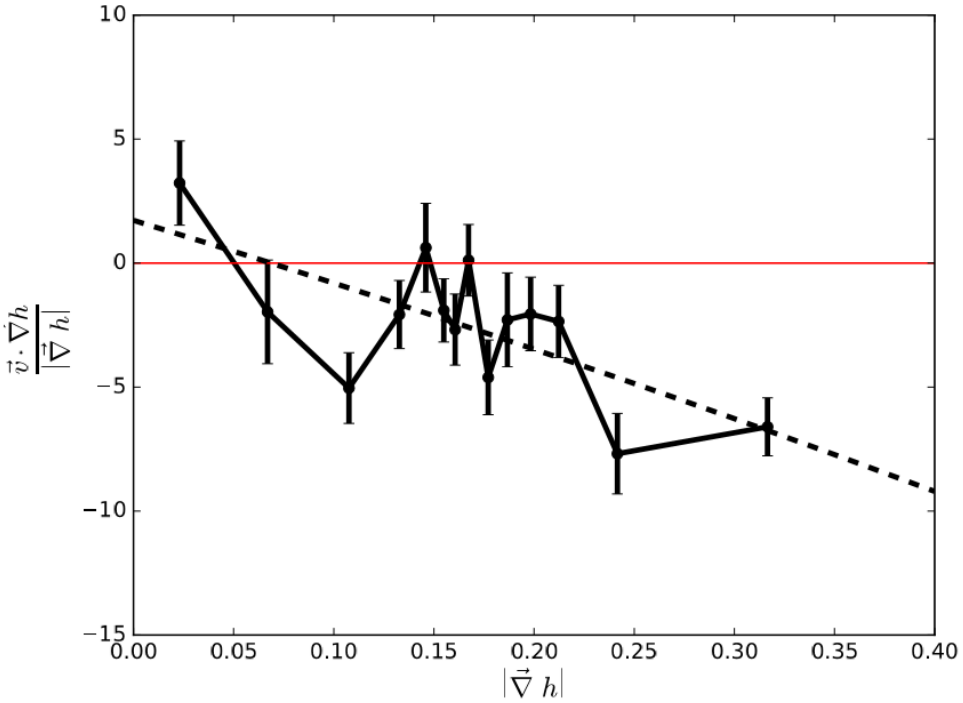


Fig. 5: The mean of the vector alignment parameter, calculated for 15 disjoint sets of measured values, as shown by the points on Fig. 4. The separation between the means in x varies because sample sizes of logs were allocated equally across the 15 sets.

Finally, we analyse the unit vectors, $\hat{u}\cdot\vec{\nabla}h$, based again on the four quartiles of the data, as shown on Fig. 4. In this case (Fig. 6), the triangular envelopes seen on Fig. 3 become strict identities, because with unit vectors $y = x\cos\theta$, with θ the angle between the log direction and the uphill direction. The counter-alignment of the log direction with the gradient direction, increasing with steeper slope, is seen in the means of the quartiles of points, joined by the heavy black line, which is similar to the result seen in Fig. 3 and 4. Both axes are dimensionless in this case.

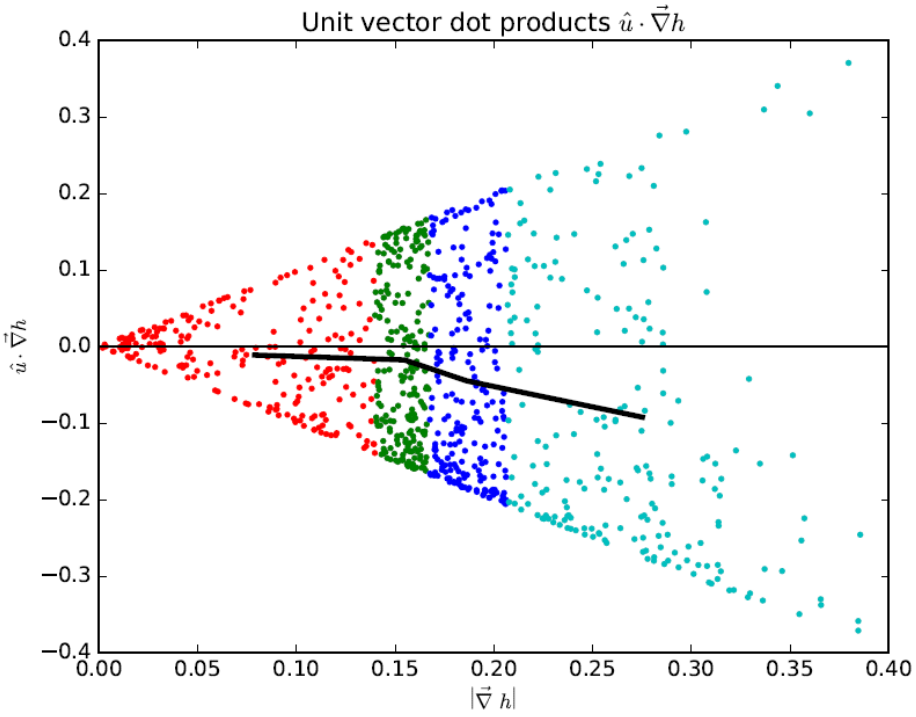


Fig. 6: The unit vector alignment parameter, $(\hat{u} \cdot \vec{\nabla} h)$. In this case the lengths of the logs are not considered, and each log becomes a unit vector with direction information only.

To Conclude

Linear features are rarely analysed using two-dimensional data from ecological plots (Dale and Fortin 2014). (The *de rigueur* approach is a statistical analysis of the spatial pattern of dimensionless points). Using a data set of logs scattered on the floor of tall eucalypt forests in Australia, we have applied the methods of vector analysis—commonly used in fields like electromagnetism to answer two simple, yet previously untested, questions: (i) do trees in a forest tend to fall downhill, and (ii) if so, is their propensity to fall downhill related to the steepness of the slope? Our answer to both questions is 'yes'!

We have established a straightforward method for efficiently measuring treefalls in forest plots and mapping the resultant data. Worldwide, the positions and sizes of trees are commonly recorded in ecological-plot networks, but the equivalent measurements of treefall are almost never collected within the same forest community (Falinski 1978, Lieberman *et al.* 1985). This is despite the important role of treefall in disturbance (including opening of canopy gaps and physical displacement of, or damage to, living trees), nutrient cycling, carbon storage, soil stability, and fire mediation (Keller and Swanson 1979, Grove and Meggs 2003, Buettel *et al.* 2017). Furthermore, measuring and mapping treefall, and considering them explicitly as linear features in forest (as distinct from single points) in spatial analyses will allow researchers to more realistically test the impact of fallen trees on the spatial pattern of the living forest . We have also demonstrated a method of mathematical analysis of these data (vector sums and dot products) that is relatively simple and intuitive; borrowed from methods of physics used on vector fields. In providing empirical support for the common-sense

notion that trees fall downhill, and that slope is an important determinant of this disturbance type, our work invites further ecological investigation of the mechanism of treefall, such as the relative importance of topographic relief versus other commonly cited factors like windthrow (Ulanova 2000) or erosion (de Toledo *et al.* 2012). That research might, in turn, have practical implications for protection of conservation forests or plantations, by improving the ability of forest scientists to target areas that require interventions to manage treefall risk or retain coarse woody debris.

CHAPTER X

INTERDISCIPLINARY TO TRANSDISCIPLINARY: SHIFTING THE COLLABORATION PARADIGM FOR GREATER ADVANCES IN SCIENCE

Ecology is inherently interdisciplinary, especially when applied outcomes are sought. Ecologists therefore are typically either trained in, or collaborate with, researchers in disciplines as diverse as statistics, physiology, chemistry, sociology, psychology and immunology. But the impetus for interdisciplinary collaborations typically arises out of necessity for particular skills rather than a desire to better understand a system. We propose that collaborative ecological research will be enriched if researchers reach further afield than these 'traditional' interdisciplinary realms, to disparate fields (e.g. physics) that ask structurally similar questions. We present a case study whereby ecological research was advanced by a collaboration with astronomers and we propose a framework by which such transdisciplinary collaborations can progress.

Introduction

Interdisciplinary research has been touted for decades (Metzger & Zare 1999) and is widely recognized as fostering the type of innovation and novelty that define exemplary science (Loeb 2016). Though obstacles exist for researchers desiring an interdisciplinary program (Rhoten & Parker 2004), interdisciplinary collaborations can offer fresh perspectives, adaptable techniques, unity of knowledge, and encouragement of out-of-the-box thinking. However, we propose that today's interdisciplinary arrangements are often done out of a sense of necessity rather than serendipity, and might not be reaching their full potential. Here we briefly review the ways interdisciplinary research is currently done, and explain how it could be enriched by reaching farther afield for collaborations. If used more broadly, such *trans*disciplinary collaborations could enrich the quality of the thinking and science produced by researchers.

The current interdisciplinary landscape and what transdisciplinary collaborations can offer

Interdisciplinarity in ecology is intensifying as scientists seek to anticipate and mitigate the current climatic and biodiversity crisis (Coreau *et al.* 2009). Tackling such broad environmental issues requires collaboration across physical, biological, social and statistical sciences (Moss *et al.* 2010), which cannot be disentangled from issues of values, equity and social justice (Pecl *et al.* 2017). Questions like "*How to make the management of the Great Barrier Reef sustainable?"* (Hughes *et al.* 2007) require interdisciplinary representation and in such cases, it is relatively straightforward to

identify what expertise will be needed, and what roles these researchers will perform. In this example, members would include policy analysts (to understand the managerial and political landscape), scientists (who can present the current state of technical knowledge on the issue, and evaluate the probability of success of a given policy), economists (to frame and analyse the cost-benefits of each scenario), and social scientists (to reflect on impacts to human well-being and challenges in securing a 'social licence' from public and private stakeholders). The *a priori* expectation is that this type of interdisciplinary effort (be it research or application) will be logistically and intellectually challenging, and will potentially expose participants to irresolvable differences of viewpoint.

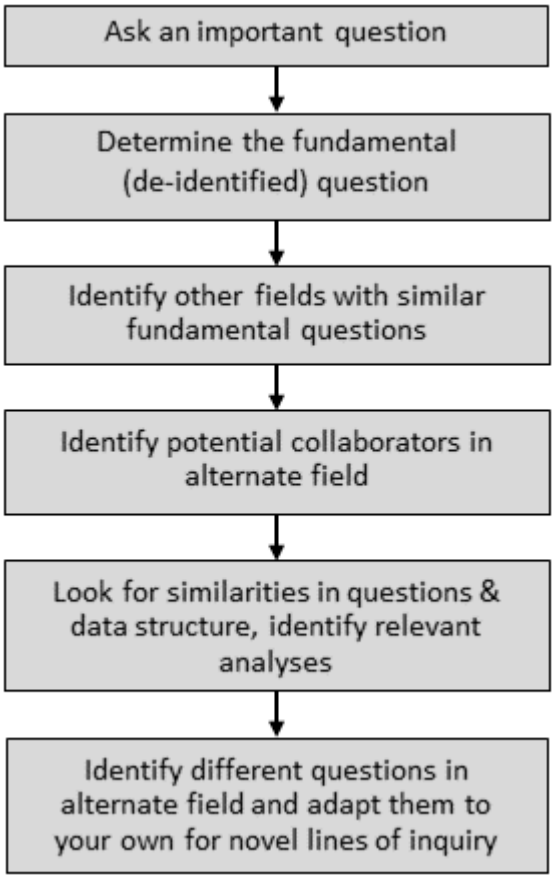
However, many have argued that all of the easy questions in ecology have been answered and all that is left are the 'wicked' problems(Churchman, 1967) : those rife with the interdependencies, uncertainties and circularities that often characterize ecological systems (Churchman, 1967). Such problems have always required interdisciplinary effort, but thus far too many of these 'wicked' problems are yet to be resolved, or indeed, mitigated (e.g., climate change). Cornell law (Lazarus, 2009) has coined these as "super wicked problems;" the longer the problem takes to be addressed/solved, the harder it will be to do so. Transdisciplinary collaborations can unlock the imagination and bring much needed perspective and novel solutions to these most diabolical of problems (Harris *et al*. 2010).

However, we ask: do we really <u>need</u> an obviously interdisciplinary problem to form a cross-disciplinary collaboration? It is well recognized that alternate viewpoints can

enhance understanding, but are we reaching far enough for alternate views? Here we suggest an alternative to the classical interdisciplinary approach; that one can instead begin with a discipline-specific data set and a restricted question (perhaps facilitated by a research student), and then seek insight from other fields. That is, flip the common approach to interdisciplinarity.

Many areas of science face logistic, inferential, economic and ethical constraints similar to ecology. For example, one can no more test the response of an old-growth forest to the introduction of an invasive species (ecology) than they can test how the human immune system will respond to a novel virus (medicine/immunology). Methods are advancing rapidly in each field to deal with these constraints but their application is often highly specific. Most researchers recognize the challenge of keeping up with the rapid progression of analytical and technological advances in one's own field, let alone the advances in other disciplines. Collaborating with experts across the range of disciplines allows a quick peek into the advances of other fields and the opportunity to adapt such techniques to the challenging and "wicked" problems of ecology. A famous example of the success of transdisciplinary thinking is (the somewhat clichéd) reference to theoretical physicist Richard Feynman taking a year off from his research on quantum mechanics to work on viruses in a Caltech genetics lab (Haynie, 2007). But what could an ecologist gain from consulting with, for instance, an astrophysicist? Such interactions, which we here refer to as *trans*disciplinary collaborations (Rosenfield, 1992), appear on the surface to be frivolous, with little apparent common ground, but can actually be a quite useful and broadening experience for all involved (see Box 1).

How to collaborate transdisciplinarily



Any transdisciplinary collaboration should begin with a well-considered and tightly specified question. Having only vague ideas risks wasted time, because there is nothing for the disparate researchers to latch on to and frame against their conceptual models. In short, such work requires the question to then be refined to its fundamental (process - or data - based) components. This process might best start from a baseline of pre-compiled datasets and a targeted problem that is discipline specific. It can then proceed by asking: "what would another scientist do, and what tools would they use if faced with identifying such patterns?" An advantage of breaking down the question is that it allows you to look for similarities and/or differences in data structure and modelling/analysis in other fields. Box 1 highlights a recent example of a transdisciplinary collaboration among forest ecologists and astronomers, and the benefits accrued by both. The key to its success was its prior investment (a graduate student's project, funding, and use of a detailed dataset), and tractable question.

The challenge for open transdisciplinary inquiry is to bring together the divergent fields and new ideas in such a way that can inform each other synergistically, rather than competing for legitimacy. For instance, in the example of Box 1, the ecologists did not require a transdisciplinary collaboration (there are many well-developed methods of spatial data analysis and modelling of patterns in forest ecology). However, pursuing this approach led to a more informative analysis, and spawned many ideas for further future research. Likewise, for an astronomical dataset (e.g., that consists of spatial point patterns, as stars or galaxies that have distinct features that can be analogous to traits of tree species. i.e., size, luminosity, age, evolutionary stage), ecologists can lend their expertise and analytical techniques. Fig. 2 outlines the general steps of undertaking a transdisciplinary collaboration.

Box 1: An example – A Forest of Stars

Such a transdisciplinary collaboration occurred among the authors of this article. Ecology researchers were grappling with a single, tangible question: "why do trees fall in a given direction?". At the root of this question was a need to understand historic processes from current patterns. The ecologists recognized that this problem is encountered by astronomers and reached across the disciplinary gulf for input.

Astronomy-Ecology links

Astronomy actually faces many problems akin to ecology (Keddy, 1994). To understand the drivers and consequences of change at the cosmic scale, Earth-bound observers use space-for-time substitution to infer dynamical processes and test theoretical models (including understanding limits and exceptions of those models). Astronomers also study the aggregate attributes of statistical populations of 'static' entities, because processes at galactic and larger scales operate on timescales far beyond the lifespan of any individual. The data obtained from telescopes represent snapshots of events that take aeons to unfold. By collating many such 'instantaneous' measures, researchers can build sequences linking the snapshots into a coherent whole. They can then test hypotheses to describe the forces and circumstances that trigger, govern, and terminate phenomena on the largest-observable scales of the Universe.

This process is analogous to many components of ecology, evolution and environmental science. Indeed, comparisons can be drawn between entities within an old growth forest, and those of a galaxy (e.g., trees as stars, species as spectral classes, ecological succession as stellar evolution, wildfire as supernova shockwaves, tree fall gaps as interstellar clouds etc). Ecology-astronomy collaborations can unveil the rules that shape the formation, maintenance and resilience of complex systems like forests or galaxies.

The process

Ecology researchers had a large dataset of all spatial locations and attributes of trees (including fallen trees) in various plots from tall eucalypt forests of Australia (www.tern.org.au/AusPlots2-pg28322.html). Through discussions with astronomers, they were able to use a program developed to infer the relative red-shift (or blue-shift) of stars from their spectral lines (current speed, trajectory and surrounding gravitational fields). The ecologists substituted trees for stars, direction of tree fall for trajectory, and elevation for gravitational fields and found that trees do indeed fall down slope, but there is a threshold of slope and size that can influence fall direction (see inset figure 1). This collaboration showed that one discipline could apply methods that innovatively speak to a dataset generated by another discipline, but more than that, it rapidly became evident that a fertilisation of new ideas quickly blossomed, and new lines of inquiry were opened to researchers in both fields.

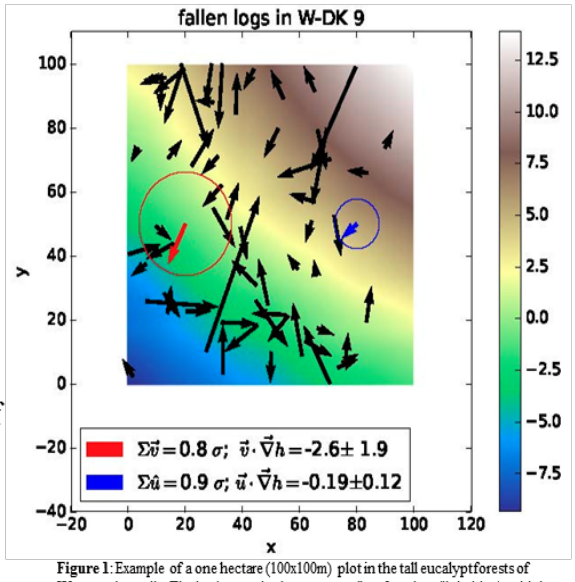


Figure 1: Example of a one hectare (100x100m) plot in the tall eucalypt forests of Western Australia. The background colours are gradient from low (light blue) to high (red-white). The black lines are the measured treefall events, including length, and the arrow is their direction.

Challenges and how to advance transdisciplinary work

Success in academia is (unfortunately) measured principally by number of publications and size of grants awarded, both of which are strongly constrained by disciplinarity (i.e., higher grant and publication success typically follows when one is considered an expert within a single discipline; Metzger 1999). This stymies creativity, collaboration and 'out-of-the-box' thinking, despite these being recognised as what many scientific fields need in order to progress (Brockman 2012). It can also be challenging to find the time to invest in a transdisciplinary approach, and resistance from some collaborators is probably inevitable. Indeed, a frequent criticism of interdisciplinary work is that it takes longer to develop/progress in the short term (due to the perceived need to develop a grounding in multiple fields), particularly within a 3-5-year funding cycle, and can be a risky career path, which explains why it is usually only entered into by either (possibly naive) graduate students or (secure) full professors (Rhoten & Parker 2004). But it is none-the-less recognised as unilaterally beneficial and, given the keen interest from early- and late-career researchers, graduate school is the perfect time to engage in such collaborations; it allows the professor to indulge their curiosity and broadens the connections and understanding of the graduate student.

Here, we have highlighted the idea that one discipline can apply methods that speak innovatively to a dataset generated by another discipline. More than that, in our experience, new ideas quickly blossomed and become interwoven with many aspects of the students' dissertation (lead author JCB). Because a tractable problem was brought to the transdisciplinary table, interactions grew organically from the bottom

up, rather than being imposed from an extensive top-down framework. A diversity of interactions evolved: discussions gave way to debates which resulted in invited lectures in each other's classes. Plots turned into models, and eventually informative analyses and co-authored papers. The potential for such transdisciplinary exchange of ideas and approaches is on offer to a suite of disciplines, not only those mentioned in our example. Even if such collaborations fail to result in joint projects and publications, those involved still have the joy of exploring novel ideas and analyses—a major underpinning of innovation and 'out of the box' thinking. In short, there is little to lose, and possibly a lot to gain, by testing the transdisciplinary waters.

CHAPTER XI

EGRESS! HOW TECHNOPHILLIA CAN REINFORCE BIOPHILIA TO IMPROVE ECOLOGICAL RESTORATION

For effective and sustained ecological restoration, community support is essential. Yet, in modern society, artificial constructs and electronic technology now dominates most peoples' interests (technophilia). This has led to a perceived growing disconnection between humans and nature. We ask how such technology might be harnessed as an agent of connection to the environment, rather than being seen as a driver of detachment. We use the example of a hugely popular mobile augmented reality smartphone game 'Ingress' to show how gaming technology can excite people about nature, unlock their inherent biophilia, and highlight the value of ecological restoration in their everyday lives.

Introduction

The increase of agricultural and economic activity in contemporary society is taking a serious toll on the living biosphere, with a large fraction of the land once occupied by nature and forests now being monopolised by people (Ellis *et al.* 2013). Many populations of animals and plants have decreased or become extinct due to human agency (Pimm *et al.* 2014), and land-use activities have led to a loss of up to 11 million km^2 of natural forest globally, in the past 300 years (Foley *et al.* 2005). The direct drivers of these biotic changes are obvious and well documented: habitat clearance and fragmentation, overexploitation, introductions of invasive species, and consequences of global change such as pollution of water and the atmosphere.

However, many also argue that the underlying reason that today's society continues to damage the environment is because not enough people care for, or place value on, nature and wilderness (Costanza *et al.* 2014). This detachment has been attributed to modern developments, including high-density urbanisation (living in the 'concrete jungle') and embedded 'digitisation' of younger generations (Dye 2008; Larson *et al.* 2011). The role of new technologies in separating us from nature is not a new phenomenon—it started with the first agricultural societies, and became a defining feature of global civilisation following the industrial and agrarian revolutions of the last three centuries (Asafu-Adjaye *et al.* 2015). In today's information and communication age, this disconnect between people and ecology is reinforced by the dearth of 'nature-based-appreciation' activities and the time spent using technology whilst living and working within climate-controlled indoor environments. This can be a confronting challenge for environmental management, because support for the

activities of ecosystem restoration and conservation is, in part, contingent on the public's awareness of human impacts and sympathy for the need to remidiate (Swart *et al.* 2001).

Bridging the human–nature divide for restoration

There are complex, well-documented challenges to restoring or conserving ecosystems, and considerable disagreement about the state to which we should restore (Higgs 2003). A successful blending of people's perception of nature with the reality of what is practically feasible, is crucial to the realisation of a unified vision on restoration goals (Davis and Slobodkin 2004, Marris 2011). However, our view of nature is partly a socio-cultural construct, constantly changing and evolving (Ellis 2015). "*There is memory of a time where the 'once natural' world emanated an essence that was thickly fragrant, unbelievably fresh, profligate, seemingly indomitable, diverse, significantly unknown, enchanted and wild*" (Crist 2004). This quote exemplifies the common (and somewhat romantic) perception of nature being something 'untouched' in a pre-human state. Yet for restoration ecology and conservation, nature is typically manifested as an anthropogenic or naturally modified system, where a pre-human state may no longer be an achievable (and perhaps not a desirable) restoration outcome. Our point here is that people's view of nature is both changing (i.e. due to a gradual shift in the social zeitgeist) and is also personally idiosyncratic; we should not expect everyone to perceive or care about nature in the same way. A return to some historical condition (e.g., pre-European, pre-Aboriginal, pre-Industrial), or the reformation of degraded landscapes to novel but functional ecosystems, are two extremes along a spectrum of possibilities that restoration

ecologists might seek to achieve (Hobbs *et al.* 2009). However, such disparity between restoration options and people's views can lead to misunderstandings among decision makers (e.g. NGOs, governments, private landholders) and difficulty in communication of restoration goals to the general public. This is problematic, because the broader community are ultimately the most important stakeholders to engage in the long-term covenant of ecosystem conservation.

People seem to have an intrinsic rapport with nature: this inherent love of living systems has been termed *biophilia*. Framed by Wilson (2007), this hypothesis seeks to explain a range of behaviours, from the simple act of keeping pets at home or potted plants in the office, to altruistic actions towards other species, sometimes going to great lengths to save individuals or conserve populations. Others, however, go about their day-to-day lives largely unaware of this affinity to nature and therefore unknowingly tend to focus on activities in artificial environments that act to stifle biophilia (Balmford *et al.* 2002). Thus the question arises: how can this care for nature be re-kindled in such a technologically-orientated society, or at least in its neglect, how can we mitigate further harm?

Outreach by ecological professionals, and citizen-science programs such as monitoring or replanting, are both commonly used to educate, inform, and engage people in critical decision-making processes about ecology. These initiatives are valuable because they promote the reconnection between people and nature, and help to improve their understanding of science (Devictor *et al.* 2010). Research on ecosystem change typically requires voluminous data spanning large spatial and temporal scales: without programs like citizen-science, much valuable environmental

research would not be possible (Silvertown 2009). New technological tools have been shown to facilitate public engagement in citizen-science, as well as improving people's enjoyment of wildlife and ecosystems (Newman *et al.* 2012). For instance, smartphone applications (apps) for bird watching, species identification keys, maps of national parks, geocaching (GPS letterboxing) and hiking or bushwalking, are now common. In contrast to classic field guides (e.g. books and brochures), these Apps can be interactive (and in some cases competitive e.g. for 'twitching'), and so create new and exciting experiences for 'nature lovers'. But such methods arguably hold little appeal to those who are 'divorced' from nature due to such reasons as apathy, or lack of awareness and opportunity.

The *biophilia* hypothesis conjectures that everyone is a potential nature lover: accepting this idea, how might we unlock this latent enthusiasm in and sympathy for ecology and wilderness? One possibility is to harness technology as an agent of connection, rather than to see it as driver of detachment. The idea here is to embrace alternatives that would appeal to the younger 'tech-savvy' generation and encourage them to be pro-active participants in the protection and restoration of ecosystems. But to engage a seemingly technophilic society, we need to focus attention on approaches that have wide appeal, attract a diverse audience, are personally rewarding, and yet also avoid detrimental associations with the environment. Moreover—and against intuition—nature appreciation might not need to be the primary goal. An example of the use of technology and Apps that shares many of these goals, and has yielded some fascinating and positive side-effects, is *Ingress* (ingress.com).

Ingress – Augmented reality for the everyday world

Ingress, a massively multiplayer smartphone app developed initially by Google, is a location-oriented game that gets its players ('agents') to interact with real-world objects that are overlain by a veneer of simulated characteristics. The game's narrative is based on the imposition of alien technology and 'exotic matter' into the world, with factions established to promote or defend against this ingression (Chess 2014). The focal elements are artificial structures such as monuments, statues, plaques and buildings of significance, including churches and architectural novelties, which serve as 'portals' that exude exotic matter and can be attacked and secured. These portals can be 'hacked' to deliver keys, weapons, shields and other inventory items, as well as 'action points' and a strategic element is developed by linking portals to create factional 'fields' of influence. Released in 2012, the player base is now huge—with over 7 million active participants and 12 million unique downloads (Takahashi 2014). This is largely due to the convenience of the smartphone—it takes advantage of the fact that mobile phones are now pervasive in modern people's lives, such that *Ingress* can be played at a whim, without need for pre-planning. In short, it is always ready.

Ingress has been lauded (and promoted by its designers) for encouraging its players to become more physically active, as well as building a sense of community by having people within factions working collectively to realise larger-scale in-game goals (Odobasic *et al.* 2013). This includes coordinated events called 'anomalies', in which hundreds of participants aggregate for a short while to pursue team objectives that would be impossible to achieve for any individual gamer (ingress.com/events). The fitness benefits arise because *Ingress* portals are spread out across a wide landscape

(typically in urban and peri-urban zones), meaning that players must walk back-and-forth between portals to develop control fields. The intrinsic link between the fictional portals (the simulated component) and actual physical structures also encourages its players to—as a side effect of the gaming—locate, recognise and identify with an array of cultural icons that they might otherwise ignore (Sheng 2013). That is, their connection to their society is enhanced as a side effect of wanting to achieve gaming goals, rather than being a direct focus of the activity. The game's newsletters also actively promote the beauty of the natural locations that players visit, via a *#IngressActualGameplayFootage* hashtag, which plays cleverly on the idea of reality being the ultimate in high graphical resolution and rendering of complex environmental textures (concepts that are important to modern gamers).

Games like *Ingress* embody a technological concept called 'mobile augmented reality' (MAR), where elements of the physical world are supplemented with portable, interactive, computer-generated attributes and synthetic sensory inputs (Richerzhagen *et al.* 2014). In this case, a smartphone or electronic tablet that provides the MAR gaming interface is used to 'paint' the local environment with graphical overlays and detect player movements based on geo-locational inputs from the device's inbuilt Global Positioning System (GPS). Beyond gaming, augmented reality has recently been applied in fields as diverse as archaeology (e.g. enabling visualisation of reconstructed ancient ruins, or the superimposition of models of buried features that have been detected by remote sensing), and sightseeing (e.g. enhancing a tourist's experience of an area via visual descriptors or even reconstructions of historical events) (Vlahakis *et al.* 2002; Etxeberria *et al.* 2012; Nunes and Mayer 2014). With the recent advent of wearable input devices such as Google Glass and the Microsoft HoloLens

headsets, which have sophisticated sensors and the capacity to blend holographic overlays directly within the visual perception range of the user (Hasan and Yu 2015), it seems inevitable that even more interesting ways will be found to meld MAR with entertainment, education, and research applications (Enyedy *et al.* 2012; Girard *et al.* 2013). Indeed, mobile augmented reality has recently been adapted as a learning tool to increase an individual's interaction with, and knowledge of, the environment (Kimiko and Alice 2013). Below we explore the idea of whether there might be an innovative role for this technology in restoration ecology.

As noted above, the developers of *Ingress* are eager to promote the health and exploratory benefits of the game (i.e. by encouraging outdoors interactions and player roaming) (Berkovsky *et al.* 2012). Yet in practical terms, the natural world serves as little more than the background panorama upon which artificial and technological features of the game are imprinted. Indeed, a defining characteristic of the focal objects in the MAR simulation (portals) is that their real-world counterparts must be created by, or at least linked intrinsically to, human society and culture. Wholly natural structures or organisms, however spectacular or iconic, are not permitted; at best, a commemorative sign or plaque that describes the feature can be considered as a portal anchor. This meshes with the plot of the game, but also probably has a practical grounding—for the MAR-overlay on the smartphone to work, the device must be within reception range of a cell tower or Wi-Fi network. However, as the ubiquity of mobile-phone coverage expands globally, this is unlikely to be major constraint in the future.

Nature as a side-effect of MAR/gaming

Now, perhaps this 'nature as a side-effect' is not such a bad thing. People who choose to play MAR games are, almost by definition, 'digitally savvy', and are arguably technophiles. A game that focuses on the impost of alien technology on contemporary society therefore has a compelling narrative for this type of entertainment consumer, and this might explain the game's popularity. It seems unlikely that this demographic would seek out nature-focused apps explicitly. But would it be possible to imagine a smartphone app (or a modification to existing apps like *Ingress*) that captures the key 'fun' features of MAR games, yet makes nature, not artificial structures, the priority goal? It might build initially on the *Ingress* theme by targeting human elements within an ecological setting (rather than a cityscape, as is most common in the current incarnation of the game), and perhaps be linked to outdoor goal-driven activities such as orienteering and trail hiking. The appeal to the app developer would be an enlivening of the content and the opening of new 'game spaces' within which to explore, map and engage—akin to the geographical 'expansion packs' for the fully digital environments realised in the massively multiplayer online role-playing game *World of Warcraft* (worldofwarcraft.com).

Ultimately, we could imagine an *Ingress*-type game that focuses explicitly on natural elements and ecological settings. The name is almost too obvious: *Egress* (definition: *the action of going out of, or leaving a[n inside] place*)! The possibilities for such an ecologically oriented apps are diverse, and might include using smart devices to photograph, geo-locate (and automatically identify) species within a landscape (e.g. 'twitching' for birds, as a game goal, with accompanying 'experience points' or skill

gains), identifying rare plants or insects, detecting signs of animal activity (diggings, droppings etc.)—all connected to an ecological narrative. Furthermore, whereas *Ingress* gameplay involves destroying the opposing faction's artificial portals and defending (and networking) those of your team, a nature-oriented MAR game could instead focus on restoration. Much as archaeology is using augmented reality to visualise ancient landscapes and structures, *Egress* could be used to 're-imagine' ecosystems of the local area as they once existed, or envisage how a restored system might appear. A key outcome would be getting people to care about protecting and restoring the part of nature that they live in, or have interacted with, because the act of playing an entertaining, nature-focused game, which includes scoring, levelling and protecting the MAR objects in this landscape, has given them a tangible and personal connection to it.

Nature in games, and games in nature

The popularity of some genres of computer games suggests that the connection between nature and player enjoyment is deep-seated, and perhaps related to biophilia. For instance, simulated worlds, such as those that form the setting for massively multiplayer online roleplaying games, typically contain vast tracts of wilderness to reconnoiter. In their milieu, the cities and towns constitute only small pockets of civilisation. Exploration and adventure within forests, mountains, and other remote environments, is a primary goal (Fuster *et al.* 2013). Furthermore, recent studies (using similar methodologies to those ecologists use to assess habitat selection) suggest that gamers in these worlds actually prefer to gather and role-play in natural-looking areas with a predominance of greenery, even when not actively exploring (Truong *et al.*

2015). Might such positive in-games experiences with the ecology of artificial universes translate into fun in the real world?

Two of the driving motivations for players—in both virtual universes and MAR games like *Ingress*—are self-improvement and social interaction. Players 'level up' by questing or completing objectives, and success can be predicated on, or at least facilitated by, cooperation with others (Granic *et al.* 2014). We argue that any *Egress*-like experience, using wild nature as its gaming canvas, should try to capture these incentives. A challenge for developers would be to link player advancement to positive interactions with ecology, rather than the standard trope of combat with wild creatures and the harvest or 'taming' of wild places. In computer-based role-playing adventures, nature is inherently resilient and is restored (refreshed to their initial state) periodically when the game servers are reset. A MAR gaming experience, embedded in real-world 'wild environments', might instead ask players to quest for unique locations, natural landmarks or habitats, detect rare species or locate as many common ones as possible, and use the augmented overlay to re-design or restore visited ecosystems to some more diverse or 'powered up' state (to borrow from the gaming lexicon). The game might also allow for players to choose (simulated) actions that are detrimental to an area's ecology or conservation values—leading to degradation rather than restoration—and then make use of the MAR interface to illustrate the plausible consequences of such decisions on their local environment. Therefore, MAR can act as a valuable tool for facilitating the learning experience of restorationists and ecologists, contributing to a shift in attitudes from a human-centric vision to one more focussed on environmental conservation and knowledge – all within the boundaries of existing human values (Manfredo *et al.* 2016). There are many such possibilities! However, the underlying

goal of making the interaction with nature fun and rewarding must be paramount, lest the experience diminish to little more than another prosaic 'educational app' for the cataloguing of plants and animals.

Conclusion

Technology cannot, in itself, resolve the vexed questions around what restoration and conservation actually is, and why and how we should do it. Where it has great potential is in the way technology can stimulate interest and engage people in constructive restoration dialogues. For instance, by using MAR games to get technophiles out into the 'wild'—their new 'gaming habitat'—a broader swathe of the public might come to care about and understand the value of ecology and conservation. Biophilia meets technophilia! Similarly, by harnessing MAR and related technologies to imagine and manipulate virtual representations, people can be armed with a more expansive vision of restoration goals, as well as a tangible visualisation of the potential of proposed actions. This would allow people to be integrated into environmental decision making in a cost effective and participatory way.

Here we have proposed the idea of an app called *Egress*, as an ecological counterpart to the wildly popular *Ingress* MAR smartphone game. Such a tool might also blend seamlessly with citizen science programs, by encouraging users to collect useful data such as identifying and geo-locating plants and animals, or taking images of ecosystems that serve as monitoring points to understand dynamic changes on daily to yearly time-frames. All while scoring points, levelling up, cooperating with friends, and enjoying themselves in nature. A win in a game can be a win for science. The

critical point is that there is no need to start from scratch—*Ingress* can serve not only as a software template for imagining the opportunities offered by an eco-focused gaming app, but also as an existing community of outdoors-MAR adherents, with its community of 7 million active players. The possibilities are boundless.

CHAPTER XII

OVERVIEW AND FUTURE DIRECTIONS

The major findings of the research thesis are reviewed, and their implications for conservation and management, in light of recent global change, are discussed. Other potential methods for research in the field of forest ecology are outlined. Finally, I envisage what future of forest ecological models might look like, and highlight the need for perseverance and innovation as we move forward into a new era of research.

The principal goals of this thesis were to critically analyse current knowledge based on forest-plot studies, and use cutting-edge research methods—underpinned by existing data bases and new field data—to improve understanding of the links between pattern and process in forest ecosystems. The focus was the tall eucalypt biome of Australia (examined in this way for the first time), but the outlook was global. The use of a combination of existing and new modelling approaches, underpinned by novel conceptual ideas, were key features of this thesis (Fig. 1). A hope is that this body of research will have impact on, and change discussion around, how future studies of pattern and process in forest ecosystems are done. A particular

ambition of mine was to seek out interdisciplinary collaborations, and use these to spark new ideas on how to conceive, measure, and interpret long-term forest dynamics from snapshots of standing pattern; this is a practical problem facing conservation managers working in forest systems worldwide. In this general discussion, I will briefly highlight and summarise the overarching themes of this doctoral thesis, given that each chapter already been evaluated in its specific context. Finally, I will sketch my vision of what a future model framework for forest ecosystem might look like.

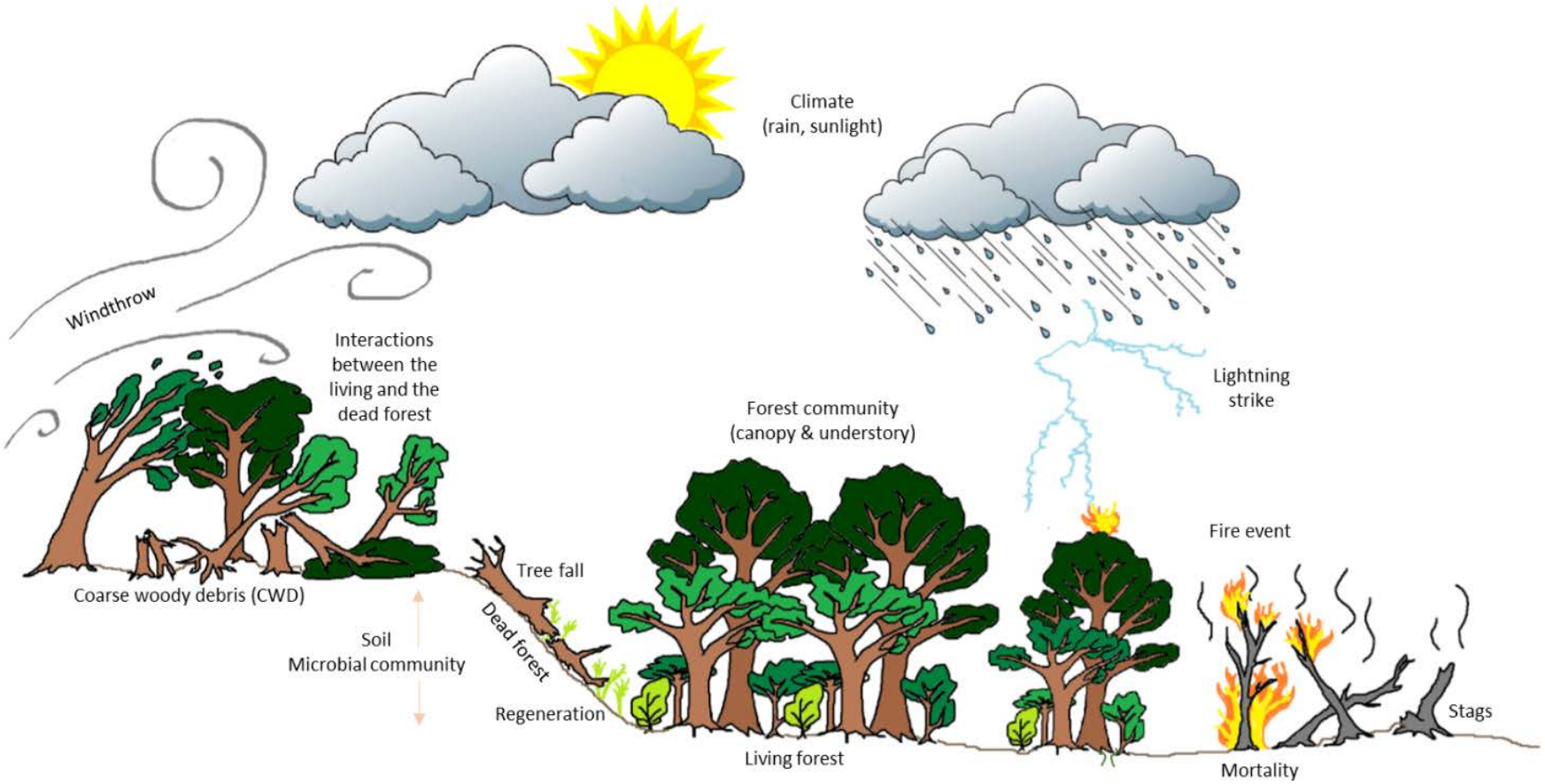


Fig. 1: Synergies among drivers of forest pattern and process. This cartoon highlights all key elements of my PhD, as well as the process that shape these elements but were not included. External forces (e.g., disturbance events) can alter attributes of a forest at any time.

The major findings and outcomes (following the order taken in the thesis) were:

- Aggregation is the dominant spatial pattern in forests worldwide.
- Reported spatial patterns are highly sensitive to a researcher's choice of methodology (size of tree measured, plot-size, and plot location). Choosing to measure the small trees of a forest (in additional to large) acts to increases the probability of detecting aggregate patterns. Future research should consider a standard protocol for study design and reporting, to minimise non-ecological influences on pattern detection, and increase cross-study comparability.
- Australian tall eucalypt forest communities exhibit more aggregate spatial patterns than random, in concordance with other forest types worldwide.
- Separating the eucalypt and non-eucalypt components when measuring and analysing Australian tall forest systems is essential for understanding the underlying processes and mechanisms that drive their patterning; eucalypts dominate the total biomass, and non-eucalypts the number of individuals.
- Eucalypt (canopy) and non-eucalypt (sub-dominant and understory) communities are decoupled; that is, the density and biomass of non-eucalypts are more predictable and explicable by climatic factors than eucalypts. It follows that disturbance events (e.g., fire) will augment climatic effects, and in some cases, impact eucalypt and non-eucalypt components differently. This has implications for how we manage and conserve eucalypt-dominated forests. Strategies need to account for this vertical stratification to be most effective.
- Fallen trees are important dynamic components of forest ecosystems, but are often overlooked in studies of pattern and process. If measured *in situ*, alterations in treefall pattern, dynamics and tree mortality may serve as early-warning flags of changes in forest structure and function.

- The dead component of forests (such as standing dead, tree falls and coarse-woody debris) should be added to the definition of what a forest is (and is not).
- Both the number of living trees, and abundance of large logs, are highly correlated with readily measurable site-based proxies of disturbance (e.g., cutting grass or fern presence/absence) in tall eucalypt forests. Dead and living wood biomass however, is difficult to explain using site-based presence/absence characteristics.
- I developed an intuitive and practical method of creating high-resolution digital elevation models (DEM) for forest plots, that is comparable, if not better than current remote sensing methods, and is not affected by canopy cover. This model can be used by anyone that has (or will collect) slope data in the field.
- New approaches are needed to encourage and facilitate interdisciplinary research. I demonstrate how new *trans*disciplinary approaches to collaboration can occur by catalysing innovation in a field by borrowing and modifying/improving standard practices from a disparate discipline.
- Through the innovative use of analytical methods taken from physics/astronomy (used commonly to study motion-vectors in star clusters) we determined that trees do indeed fall down slope, and that the steeper the gradient of the slope, the greater the propensity for tree fall in that direction.
- Conservation and restoration initiatives should better harness existing technology (e.g., app-based gaming, with a large mobile audience) to educate and encourage the general public to get outdoors and experience nature.

Future directions

1) Make data available

Ecology is an integrative discipline, generally requiring the collection of large volumes of data (Hampton *et al.* 2013). However, analyses and comparisons between different regions are often hampered by insufficient data, particularly covering long time-scales. Underscoring this problem, it has been estimated that <1% of the ecological data that has been collected was made accessible after publication, much less in a usable form (Reichman *et al.* 2011). Often, published papers represent the underlying data in an interpretative format that fails to fully capture the richness of the underlying data (Heidorn 2008). Access to data, information and knowledge is not only important for improving our theory and models of how ecosystems function and are maintained, but is also crucial for validating methods used to tackle the profound environmental concerns we face today. The data that was collected through AusPlots forests will be made publicly available at the conclusion of my Ph.D. candidature, as will all tree fall data that I collected, and code that I developed (portal.tern.org.au).

2) Standardised reporting of results and analyses

Of the data that is available for forest ecosystems, there is little consistency in what is reported. Our ability to address questions at larger spatial scales and over long-time frames depends on our ability to compare and critique studies (Hillebrand and Gurevitch 2013), which is not just an issue for ecological studies. Greater consistency in the metrics analysed and reported will ensure future studies are methodologically comparable and geographically unbiased. One such initiative, 'CTFS-ForestGEO',

has recently been established (Anderson-Teixeira *et al.* 2015). It aims to yield insights on how and why forests are changing using a dataset compiled from multiple large (>25 ha) plots using standardised protocols. Yet, to date, only a few of the CTFS plots have made their data publicly available (refer to point 1). Progression of knowledge requires reproducible data that can be verified, stress tested, and built upon.

3) Do not go it alone

The problem of tracking dynamical change in spatio-temporally complex systems like forests is a challenge that is difficult to solve for individual researchers, but efforts to embrace the collective work of many ecologists (like the CTFS initiative described in point 2), gives encouragement that future research may be armed collectively with better tools and ammunition for facing future environmental challenges. Collaborating with a network of researchers also increases the likelihood that individuals are interpreting the data in a systematic and comprehensive way (see point 1). Furthermore, collaboration facilitates the amalgamation of heterogeneous datasets that can potentially be used to address larger scale differences—or in the case of transdisciplinarity, results in the same questions being analysed using a variety of different analytical and conceptual methods, enriching the interpretation process.

4) Further develop understanding of treefall

As has been mentioned in various chapters throughout this thesis, the dead wood is an important component of forest structure and dynamics. There are many ways in which their role in landscape ecology can be explored further. Future analyses could consider

applying fibre point-process methods (Foxall and Baddeley, 2002; Dale and Fortin 2014), coupled with the mapping method I developed in Chapter IX as a baseline, analyse the potential interaction between the logs and the living trees. The hypothesis here would be that the logs have a strong influence on the pattern and structure of the forest both during, and after, the treefall event (e.g., treefalls are more probable where density of trees is higher). Current spatial statistics would consider 'gaps' in the landscape as repulsion (presence of competition) between individual trees when, in reality, the gap might have been generated by a tree fall event, and the absence of trees merely represents the presence of an occluding structural feature (the log). The derivation of robust summary metrics for landscape, aspatial and spatial patterns in data is important for the purpose of description, but is also a crucial benchmark against which synthetic data generated by simulation models of the forests can be validated (van der Vaart *et al.* 2015). The primary aim of exploring these interactions would be to include the standing dead and fallen logs in future simulation models.

5) Analysis and model development

Forests are complex systems (Filotas *et al.* 2014) and if the spatio-temporal dynamics of individual trees are to be represented adequately in models, a rigorous, bottom-up approach is needed. All models are, by definition, simplified caricatures of actual ecological systems, with potentially unrealistic assumptions, but they offer the advantage of allowing for the low-cost testing of competing predictive theories in a fully controlled and replicated environment, with outcomes that are measured precisely (Peck 2004). Although not statements of truth, model outcomes can lead to specific predictions (e.g., on functional traits) that field research can later verify (or

falsify). I was unable to develop the full simulation model that I argued was necessary in the *Introduction* (Chapter I) of this thesis. From the outset, it became apparent that there was (and still is) so much that we still do not understand about forest pattern and process, and our knowledge base is a fundamental first step before realistic models can be developed. I did highlight, in Chapter VII, the output from a simple aspatial model of forest turnover (which included size-structured living trees, standing dead and logs); this was used to illustrate patterns of degradation in forest ecosystems. Future research could aim to extend this basic approach, fitting parameters of stochastic, dynamic individual-based simulation models to point-pattern summary statistics (Lehmann and Huth 2015). Multivariate spatial data can provide important additional layers of information for validating the signals of process based on a multi-focal view of pattern observations (Illian *et al.* 2009, Hartig *et al.* 2011, Illian *et al.* 2013, May *et al.* 2015). The objective underlying modelling and simulation is to generate patterns that emerge under the assumption of a set of bottom-up driving processes (Schroder and Seppelt 2006). Based on knowledge on the relevant mechanisms shaping a system (such as I have done in this thesis), one can set up simulation models using a plethora of methodologies, from aspatial cohorts, to multi-layer cellular automata, to sophisticated agent-based models (e.g., Railsback and Grimm 2012; DeAngelis and Grimm 2013; Shifley *et al.* 2017). Such models might superficially look like the assortment of patterns illustrated in the AusPlots forest maps shown in fig. 2.

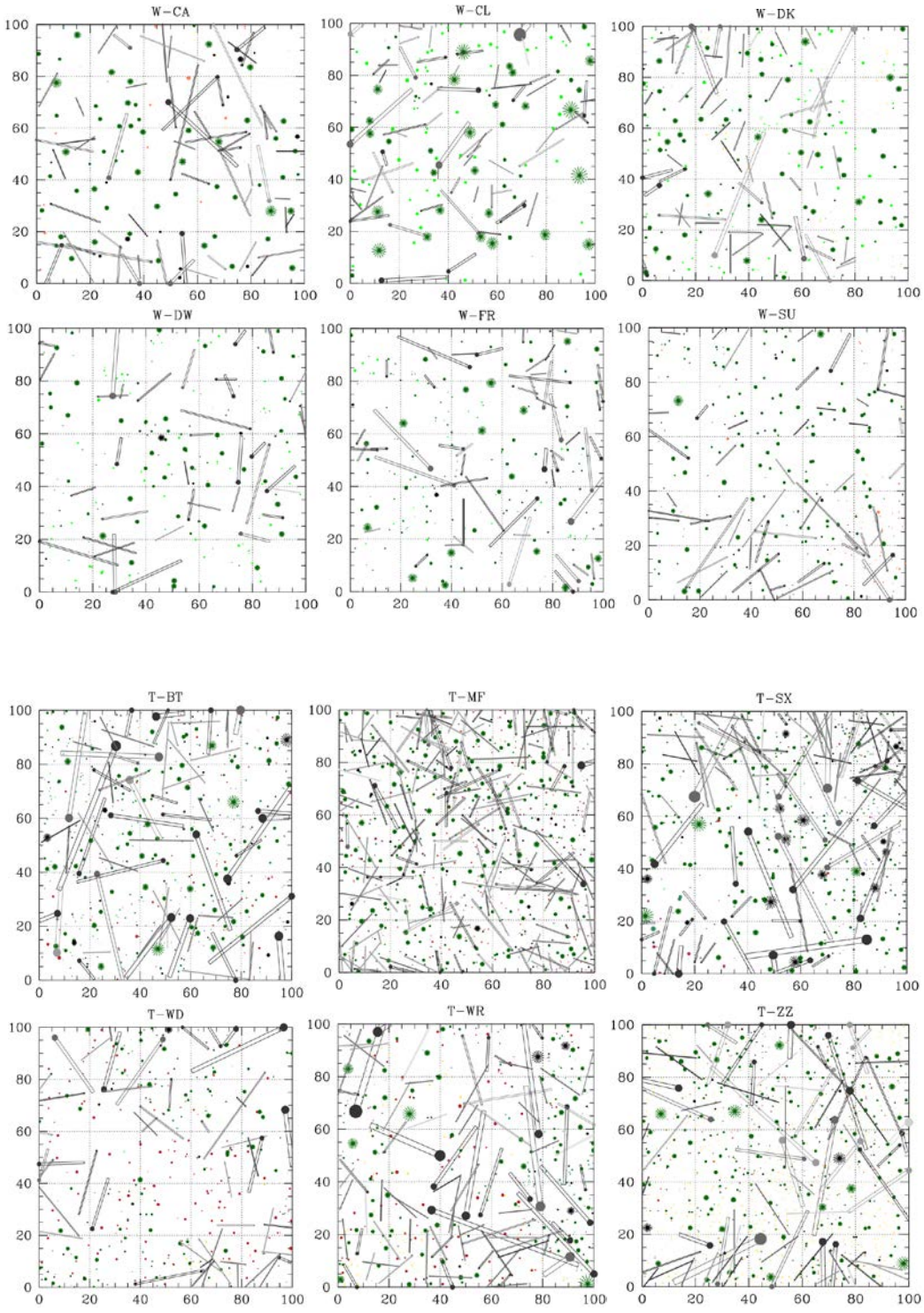


Fig. 2: Example forest plots showing the diverse array of structural and spatial variables that can be represented in a dynamic simulation model. Included are the fallen trees (their base point shown by the dark circles) and the living trees of different size, age, species and density (coloured dots and symbols).

Developing a plot-level model would serve to summarise attributes as scalars, vectors and matrices, divided broadly into biotic (variable by definition, but covering a wide span of time scales), abiotic fixed, and abiotic variable processes. Examples might include number of trees of a given species (biotic scalar), average slope (fixed abiotic scalar), size distribution of trees for each species (biotic vector), state of surface water (dry, muddy, flowing, etc.: variable abiotic vector). Patterns would be derived from snap-shots of attributes (e.g., basal area of living trees) or trends in them (e.g., change in number of species over time, for plots monitored with repeated measures). Processes would be represented by defined intrinsic relationship between attributes (e.g., self-thinning rules leading to changes in number of individual trees and their basal area) and the influence of extrinsic events or trends on attributes and intrinsic processes (e.g., fire events, antecedent rainfall, etc.). These deterministic and stochastic processes drive the dynamics of the system, while the response is dictated by the state/pattern of the attributes, the accumulation of changes, and feedbacks.

A finer-scale simulation model of AusPlots, using (for instance) an array of 20 m (25 cells) or 2m (5,000) gridded lattices, occupies the same intellectual ground as the plot-level (single 100m cell) model, but would represent increased detail on (or introduction of new) attributes, processes and derived patterns. As we move from the coarse to fine scale, the key question that needs to be considered in the new design is: what level of abstraction can be relaxed by now that a new degree of spatial resolution has been allowed. For instance, at the subplot-level, crude gradients in basal area or species richness could be derived, but the spatial characteristics of individual trees would still be ‘invisible’ to the model. For the 2m-scale model, by contrast, each tree above a threshold size would occupy (or not) a grid cell, and spatial competition, point-

patterns of aggregation, for example, could be captured explicitly and analysed, and be simulated to influence fine-scale processes that determine the system's evolution.

An analogy: Imagine viewing the planet Jupiter from Earth. With the naked eye, we see a bright and effectively dimensionless star; the only detail we can observe is its colour and brightness. When we train our binoculars on it, however, we see a two-dimensional disc, with four orbiting pinpoints of lights [the Galilean moons], and perhaps a hint of surface features. We then point a telescope at Jupiter and through an eyepiece can make out spatial features on an enlarged disc, including cloud bands, the Great Red Spot, etc. We then fit a planetary camera to our telescope and, after stacking and processing many video frames, reveal more fine-grained details of swirling eddies, subtle differences in colour between the bands and zones, a rotation of the disc over time. Finally, we look at images and data collected by spacecraft like the Juno mission, and note information on cloud depth, temperature profiles in the atmosphere, magnetic field intensity, etc. The point is that the planet has not changed, but our perception of the detail and complexity has increased, as we 'zoom' closer and improve our instruments and measurements. *Photo credit: Barry Brook, Huon Ridge Observatory,*

Final remarks

In this thesis, I report on the links between pattern and process in the tall eucalypt forests of Australia, and by doing so, have improved our understanding of the fundamental processes influencing forest structure and function. My motivation throughout this candidature was to make a significant contribution to the field of forest ecology. I did this by exploring solutions to decadal problems (such as definitions) and innovating ways in which we can apply research both conceptually and practically. The future of research in environmental science is still rich and rewarding, I believe we just have to continue to think outside-the-box, seek collaborations further afield and just do science.

REFERENCES

Aakala, T., Kuuluvainen, T., De Grandpre, L. & Gauthier, S. (2007) Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. *Canadian Journal of Forest Research,* **37,** 50-61.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* **259,** 660-684.

Alroy, J. (2015) The shape of terrestrial abundance distributions. *Science Advances,* **1,** e1500082.

Alroy, J. (2017) Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of the National Academy of Sciences of the United States of America,* 201611855.

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A. & Baltzer, J.L. (2015) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology,* **21,** 528-549.

Arevalo, J.R. & Fernandez-Palacios, J.M. (1998) Treefall gap characteristics and regeneration in the laurel forest of Tenerife. *Journal of Vegetation Science,* **9,** 297-306.

Asafu-Adjaye, J., Blomqvist, L., Brook, B.W., Brand, S., De Fries, R., Ellis, E.C., Foreman, C., Keith, D., Lewis, M., Lynas, M., Nordhaus, T., Pielke Jr, R., Pritzker, R., Roy, J., Sagoff, M., Shellenberger, M., Stone, R. & Teague, P. (2015) *An Ecomodernist Manifesto.* http://ecomodernism.org/manifesto.

Ashton, D. & Attiwill, P. (1994) Tall open-forests. *Australian Vegetation* (ed S. Groves), pp. 157-196. Cambridge University Press, London.

Attiwill, P.M. (1994) The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management*, **63,** 247-300.

Attiwill, P.M. (1994) Ecological disturbance and the conservative management of eucalypt forests in Australia. *Forest Ecology and Management*, **63,** 301-346.

Bader, M.Y. & Ruijten, J.J.A. (2008) A topography-based model of forest cover at the alpine tree line in the tropical Andes. *J Biogeogr*, **35,** 711-723.

Balmford, A., Clegg, L., Coulson, T. & Taylor, J. (2002) Why conservationists should heed Pokémon. *Science*, **295,** 2367-2367.

Bassett, M., Chia, E.K., Leonard, S.W.J., Nimmo, D.G., Holland, G.J., Ritchie, E.G., Clarke, M.F. & Bennett, A.F. (2015) The effects of topographic variation and the fire regime on coarse woody debris: Insights from a large wildfire. *Forest Ecology and Management*, **340,** 126-134.

Berkovsky, S., Freyne, J. & Coombe, M. (2012) Physical activity motivating games: be active and get your own reward. *ACM Transactions on Computer-Human Interaction*, **19,** doi:10.1145/2395131.2395139.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C. & Gegout, J.-C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479,** 517-520.

Bielewicz, P., Eriksen, H.K., Banday, A.J., Górski, K.M. & Lilje, P.B. (2005) Multipole vector anomalies in the first-year WMAP data: a cut-sky analysis. *The Astrophysical Journal*, **635,** 750.

Blanchard, S.D., Jakubowski, M.K. & Kelly, M. (2011) Object-based image analysis of downed logs in disturbed forested landscapes using LiDAR. *Remote Sensing*, **3,** 2420.

Bonan, G.B. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320,** 1444-1449.

Bongers, F., Poorter, L., Van Rompaey, R.S.A.R. & Parren, M.P.E. (1999) Distribution of twelve moist forest canopy tree species in Liberia and Côte d'Ivoire: response

curves to a climatic gradient. *Journal of Vegetation Science,* **10,** 371-382.

Bosse, M., Zlot, R. & Flick, P. (2012) Zebedee: design of a spring-mounted 3-D range sensor with application to mobile mapping. *IEEE Transactions on Robotics,* **28,** 1104-1119.

Boswijk, G., Fowler, A., Palmer, J., Fenwick, P., Hogg, A., Lorrey, A. & Wunder, J. (2014) The late Holocene kauri chronology: assessing the potential of a 4500-year record for palaeoclimate reconstruction. *Quaternary Science Reviews,* **90,** 128-142.

Bowman, D. & Kirkpatrick, J. (1986) Establishment, suppression and growth of *Eucalyptus delegatensis* R.T. Baker in multiaged forests .III. Intraspecific allelopathy, competition between adult and juvenile for moisture and nutrients, and frost damage to seedlings. *Australian Journal of Botany,* **34,** 81-94.

Bowman, D.M.J.S., Perry, G.L.W. & Marston, J.B. (2015) Feedbacks and landscape-level vegetation dynamics. *Trends in Ecology & Evolution,* **30,** 255-260.

Bradford, M.G., Murphy, H.T., Ford, A.J., Hogan, D.L. & Metcalfe, D.J. (2014) Long-term stem inventory data from tropical rain forest plots in Australia. *Ecology,* **95,** 2362-2362.

Bradstock, R.A. (2010) A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography,* **19,** 145-158.

Brasington, J., Langham, J. & Rumsby, B. (2003) Methodological sensitivity of morphometric estimates of coarse fluvial sediment transport. *Geomorphology,* **53,** 299-316.

Bretz-Guby, N.A. & Dobbertin, M. (1996) Quantitative estimates of coarse woody debris and standing dead trees in selected Swiss forests. *Global Ecology and Biogeography Letters,* **5,** 327-341.

Brockman, J. (2012) *This Will Make You Smarter.* Harper Perennial, New York.

Brokaw, N.V.L. (1985) Gap-phase regeneration in tropical forests. *Ecology,* **66,**

682-687.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M. & Anthelme, F. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96,** 18-34.

Brown, C., Law, R., Illian, J.B. & Burslem, D.F.R.P. (2011) Linking ecological processes with spatial and non-spatial patterns in plant communities. *Journal of Ecology*, **99,** 1402-1414.

Brown, J.H. (2014) Why are there so many species in the tropics? *J Biogeogr*, **41,** 8-22.

Brown, M. (2010) *How I Killed Pluto and Why It Had It Coming.* Spiegel & Grau, New York.

Brunthaler, A., Reid, M.J., Falcke, H., Greenhill, L.J., & Henkel, C. (2005). The Geometric Distance and Proper Motion of the Triangulum Galaxy (M33). *Science*, **307**, 1440-1443.

Buettel, J.C., Ondei, S. & Brook, B.W. (2017) Look down to see what's up: a systematic overview of treefall dynamics in forests. *Forests*, **8,** 123.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* Springer Science & Business Media, New York.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology*, **78,** 1958-1965.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, **20,** 620-631.

Canham, C.D. & Loucks, O.L. (1984) Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology*, **65,** 803-809.

Cannas, S.A., Páez, S.A. & Marco, D.E. (1999) Modeling plant spread in forest ecology using cellular automata. *Computer Physics Communications,* **121,** 131-135.

Chang, K.-t. & Tsai, B.-w. (1991) The effect of DEM resolution on slope and aspect mapping. *Cartography and Geographic Information Systems,* **18,** 69-77.

Chave, J. (1999) Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling,* **124,** 233-254.

Chazdon, R.L., Brancalion, P.H., Laestadius, L., Bennett-Curry, A., Buckingham, K., Kumar, C., Moll-Rocek, J., Vieira, I.C. & Wilson, S.J. (2016) When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio,* **45,** 538-50.

Chećko, E., Jaroszewicz, B., Olejniczak, K. & Kwiatkowska-Falińska, A.J. (2015) The importance of coarse woody debris for vascular plants in temperate mixed deciduous forests 1. *Canadian Journal of Forest Research,* **45,** 1154-1163.

Chen, J.Q., Song, B., Rudnicki, M., Moeur, M., Bible, K., North, M., Shaw, D.C., Franklin, J.F. & Braun, D.M. (2004) Spatial relationship of biomass and species distribution in an old-growth Psuedotsuga-Tsuga forest. *Forest Science,* **50,** 364-375.

Cheng, X., Han, H., Kang, F., Song, Y. & Liu, K. (2014) Point pattern analysis of different life stages of *Quercus liaotungensis* in Lingkong Mountain, Shanxi Province, China. *Journal of Plant Interactions,* **9,** 233-240.

Chess, S. (2014) Augmented regionalism: Ingress as geomediated gaming narrative. *Information Communication & Society,* **17,** 1105-1117.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management,* **210,** 267-282.

Churchman, C.W. (1967) Wicked problems. *Management Science,* **14,** B141-B142.

Clark, C., Poulsen, J., Bolker, B., Connor, E. & Parker, V. (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology,* **86,** 2684-2694.

Clark, J.S., Bell, D.M., Hersh, M.H. & Nichols, L. (2011) Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology,* **17,** 1834-1849.

Comita, L.S., Condit, R. & Hubbell, S.P. (2007) Developmental changes in habitat associations of tropical trees. *Journal of Ecology,* **95,** 482-492.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R. & Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science,* **288,** 1414-1418.

Coomes, D.A., Flores, O., Holdaway, R., Jucker, T., Lines, E.R. & Vanderwel, M.C. (2014) Wood production response to climate change will depend critically on forest composition and structure. *Global Change Biology*, **20,** 3632-3645.

Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs,* **70,** 171-207.

Coops, N.C., Wulder, M.A., Culvenor, D.S. & St-Onge, B. (2004) Comparison of forest attributes extracted from fine spatial resolution multispectral and lidar data. *Canadian Journal of Remote Sensing,* **30,** 855-866.

Coreau, A., Pinay, G., Thompson, J.D., Cheptou, P.O. & Mermet, L. (2009) The rise of research on futures in ecology: rebalancing scenarios and predictions. *Ecology Letters,* **12,** 1277-1286.

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S. & Turner, R.K. (2014) Changes in the global value of ecosystem services. *Global Environmental Change,* **26,** 152-158.

Cousins, S.J.M., Battles, J.J., Sanders, J.E. & York, R.A. (2015) Decay patterns and carbon density of standing dead trees in California mixed conifer forests. *Forest Ecology and Management,* **353,** 136-147.

Crist, E. (2004) Against the social construction of nature and wilderness. *Environmental Ethics,* **26,** 5-24.

Dale, M.R. & Fortin, M.-J. (2014) *Spatial Analysis: A Guide for Ecologists.* Cambridge University Press, London.

Davis, M. & Slobodkin, L.B. (2004) Restoration Ecology: the challenge of social values and expectations.(Forum). *Frontiers in Ecology and the Environment*, **2,** 43-38.

de Toledo, J.J., Magnusson, W.E., Castilho, C.V. & Nascimento, H.E.M. (2012) Tree mode of death in Central Amazonia: effects of soil and topography on tree mortality associated with storm disturbances. *Forest Ecology and Management,* **263,** 253-261.

DeAngelis, D.L. & Grimm, V. (2013) Individual-based models in ecology after four decades. *F1000prime reports,* **6,** 39-39.

Del Grosso, S.J., Parton, W.J., Mosier, A.R., Holland, E.A., Pendall, E., Schimel, D.S. & Ojima, D.S. (2005) Modeling soil CO_2 emissions from ecosystems. *Biogeochemistry*, **73,** 71-91.

Devictor, V., Whittaker, R.J. & Beltrame, C. (2010) Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions,* **16,** 354-362.

Dixon, R.K., Brown, S., Houghton, R.e.a., Solomon, A., Trexler, M. & Wisniewski, J. (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263,** 185-189.

Dungan, J.L., Perry, J., Dale, M., Legendre, P., Citron-Pousty, S., Fortin, M.J., Jakomulska, A., Miriti, M. & Rosenberg, M. (2002) A balanced view of scale in spatial statistical analysis. *Ecography*, **25,** 626-640.

Dutta, R., Das, A. & Aryal, J. (2016) Big data integration shows Australian bush-fire frequency is increasing significantly. *Royal Society Open Science*, **3**.

Duyker, E. & Duyker, M. (2006) *Bruny d'Entrecasteaux: Voyage to Australia and the Pacific 1791—1793.* Miegunyah/Melbourne University Press, Melbourne.

Dye, C. (2008) Health and urban living. *Science,* **319,** 766-769.

Ehrenfeld, J.G. (1995) Microtopography and vegetation in Atlantic white cedar swamps:

the effects of natural disturbances. *Canadian Journal of Botany,* **73,** 474-484.

Ellis, E.C. (2015) Ecology in an anthropogenic biosphere. *Ecological Monographs,* **85,** 287-331.

Ellis, E.C., Kaplan, J.O., Fuller, D.Q., Vavrus, S., Klein Goldewijk, K. & Verburg, P.H. (2013) Used planet: A global history. *Proceedings of the National Academy of Sciences of the United States of America,* **110,** 7978-7985.

Enquist, B.J. & Niklas, K.J. (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science,* **295,** 1517-1520.

Enyedy, N., Danish, J.A., Delacruz, G. & Kumar, M. (2012) Learning physics through play in an augmented reality environment. *International Journal of Computer-Supported Collaborative Learning,* **7,** 347-378.

Erdogan, S. (2009) A comparision of interpolation methods for producing digital elevation models at the field scale. *Earth Surface Processes and Landforms,* **34,** 366-376.

Etxeberria, A.I., Asensio, M., Vicent, N. & Cuenca, J.M. (2012) Mobile devices: a tool for tourism and learning at archaeological sites. *International Journal of Web Based Communities,* **8,** 57-72.

Everham, E.M. & Brokaw, N.V.L. (1996) Forest damage and recovery from catastrophic wind. *The Botanical Review,* **62,** 113-185.

Falinski, J.B. (1978) Uprooted trees, their distribution and influence in the primeval forest biotope. *Vegetatio,* **38,** 175-183.

Fangliang, H., Legendre, P. & LaFrankie, J.V. (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. *Journal of Vegetation Science,* **8,** 105-114.

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D. & Alsdorf, D. (2007) The Shuttle Radar Topography Mission. *Reviews of Geophysics,* **45,** n/a-n/a.

Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology,* **98,** 106-116.

Filotas, E., Parrott, L., Burton, P.J., Chazdon, R.L., Coates, K.D., Coll, L., Haeussler, S., Martin, K., Nocentini, S. & Puettmann, K.J. (2014) Viewing forests through the lens of complex systems science. *Ecosphere,* **5,** 1-23.

Fisher, B.L., Howe, H.F. & Wright, S.J. (1991) Survival and growth of *Virola surinamensis* yearlings - water augmentation in gap and understory. *Oecologia,* **86,** 292-297.

Fisher, P.F. & Tate, N.J. (2006) Causes and consequences of error in digital elevation models. *Progress in Physical Geography,* **30,** 467-489.

Fitzgerald, P. (2002) Tectonics and landscape evolution of the Antarctic plate since the breakup of Gondwana, with an emphasis on the West Antarctic Rift System and the Transantarctic Mountains. *Royal Society of New Zealand Bulletin,* **35,** 453-469.

Flower, C.E. & Gonzalez-Meler, M.A. (2015) Responses of temperate forest productivity to insect and pathogen disturbances. *Annual Review of Plant Biology,* **66,** 547-569.

Foley, J.A., Asner, G.P., Costa, M.H., Coe, M.T., DeFries, R., Gibbs, H.K., Howard, E.A., Olson, S., Patz, J. & Ramankutty, N. (2007) Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment,* **5,** 25-32.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science,* **309,** 570-4.

Food and Agriculture Organisation (2012) Forest Resources Assessment: Terms and Definitions of Forests. (ed K. MacDicken). Rome.

Foxall, R. & Baddeley, A. (2002) Nonparametric measures of association between a spatial point process and a random set, with geological applications. *Applied Statistics,* **51,** 165-182.

Franklin, J.F., Shugart, H.H. & Harmon, M.E. (1987) Tree death as an ecological process. *BioScience,* **37,** 550-556.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management,* **155,** 399-423.

Franklin, S.E. (2001) *Remote Sensing for Sustainable Forest Management.* CRC Press, Boca Raton, Florida.

Fraser, L.H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., Bartha, S., Beierkuhnlein, C., Bennett, J.A. & Bittel, A. (2015) Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science*, **349,** 302-305.

Frelich, L.E. & Reich, P.B. (1995) Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs*, **65,** 325-346.

Fridman, J. & Walheim, M. (2000) Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management,* **131,** 23-36.

Friis, I.B. (1992) *Forests and Forest Trees of Northeast Tropical Africa: Their Natural Habitats and Distribution Patterns in Ethiopia, Djibouti and Somalia.* HMSO, London.

Frisch, P.C., Andersson, B.-G., Berdyugin, A., Piirola, V., DeMajistre, R., Funsten, H.O., Magalhaes, A.M., Sericopi, D.B., McComas, D.J., Schwadron, N.A., Slavin, J.D., & Wiktorowicz, S.J. (2012). The Interstellar Magnetic Field Close to the Sun. II. *Astrophysical Journal*, **760**, 106-123.

Frolking, S., Palace, M.W., Clark, D.B., Chambers, J.Q., Shugart, H.H. & Hurtt, G.C. (2009) Forest disturbance and recovery: A general review in the context of

spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *Journal of Geophysical Research: Biogeosciences,* **114,** G2.

Fuster, H., Carbonell, X., Chamarro, A. & Oberst, U. (2013) Interaction with the game and motivation among players of massively multiplayer online role-playing games. *Spanish Journal of Psychology*, **16**.

Ganey, J.L., Bird, B.J., Baggett, L.S. & Jenness, J.S. (2015) Density of large snags and logs in northern Arizona mixed-conifer and ponderosa pine forests. *Forest Science,* **61,** 353-362.

Gao, J. (1997) Resolution and accuracy of terrain representation by grid DEMs at a micro-scale. *International Journal of Geographical Information Science,* **11,** 199-212.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A. & Sodhi, N.S. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters,* **12,** 561-582.

Gentry, A.H. (1992) Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos*, **63,** 19-28.

Getzin, S., Wiegand, T., Wiegand, K. & He, F. (2008) Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology*, **96,** 807-820.

Getzin, S., Worbes, M., Wiegand, T. & Wiegand, K. (2011) Size dominance regulates tree spacing more than competition within height classes in tropical Cameroon. *Journal of Tropical Ecology,* **27,** 93-102.

Ghazoul, J., Burivalova, Z., Garcia-Ulloa, J. & King, L.A. (2015) Conceptualizing forest degradation. *Trends in Ecology & Evolution*, **30,** 622-32.

Gibson, N. & Brown, M.J. (1991) The ecology of *Lagarostrobos franklinii* (Hook.f.) Quinn (Podocarpaceae) in Tasmania. 2. Population structure and spatial pattern. *Australian Journal of Ecology*, **16,** 223-229.

Gill, A.M. (1997) Eucalypts and fires: interdependent or independent. *Eucalypt Ecology: Individuals to Ecosystems* (eds J. Woinarski & J. Williams), pp.

151-167.

Gill, A.M., Groves, R.H. & Noble, I.R. (1981) *Fire and the Australian biota.* Australian Academy of Science, Canberra.

Girard, C., Ecalle, J. & Magnan, A. (2013) Serious games as new educational tools: how effective are they? A meta-analysis of recent studies. *Journal of Computer Assisted Learning,* **29,** 207-219.

Gnonlonfoun, I., Glèlè Kakaï, R., Salako, V., Assogbadjo, A. & Ouédraogo, A. (2015) Structural analysis of regeneration in tropical dense forest: combined effect of plot and spatial distribution patterns. *Acta Botanica Gallica,* **162,** 79-87.

Gong, J., Li, Z., Zhu, Q., Sui, H. & Zhou, Y. (2000) Effects of various factors on the accuracy of DEMs: an intensive experimental investigation. *Photogrammetric Engineering & Remote Sensing,* **66,** 1113-1117.

Goreaud, F. & Pélissier, R. (1999) On explicit formulas of edge effect correction for Ripley's K-function. *Journal of Vegetation Science,* **10,** 433-438.

Granic, I., Lobel, A. & Engels, R.C.M.E. (2014) The benefits of playing video games. *American Psychologist,* **69,** 66-78.

Grimm, V. & Railsback, S.F. (2012) Pattern-oriented modelling: a 'multi-scope'for predictive systems ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **367,** 298-310.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T. & DeAngelis, D.L. (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science,* **310,** 987-991.

Grove, S. & Meggs, J. (2003) Coarse woody debris, biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. *Australian Forestry,* **66,** 258-272.

Guo, Q., Li, W., Yu, H. & Alvarez, O. (2010) Effects of topographic variability and lidar sampling density on several DEM interpolation methods. *Photogrammetric*

Engineering & Remote Sensing, **76,** 701-712.

Hampton, S.E., Strasser, C.A., Tewksbury, J.J., Gram, W.K., Budden, A.E., Batcheller, A.L., Duke, C.S. & Porter, J.H. (2013) Big data and the future of ecology. *Frontiers in Ecology and the Environment,* **11,** 156-162.

Harmon, M.E. & Franklin, J.F. (1989) Tree seedlings on logs in Picae-Tsuga forests of Oregon and Washington. *Ecology***,** 48-59.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S., Lattin, J., Anderson, N., Cline, S., Aumen, N. & Sedell, J. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research,* **15,** 302.

Harmon, M.E. & Hua, C. (1991) Coarse woody debris dynamics in two old-growth ecosystems. *BioScience,* **41,** 604-610.

Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology,* **89,** 947-959.

Harris, J., Brown, V.A. & Russell, J. (2010) *Tackling Wicked Problems: Through the Transdisciplinary Imagination.* Earthscan, New York.

Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T. & Huth, A. (2011) Statistical inference for stochastic simulation models–theory and application. *Ecology Letters,* **14,** 816-827.

Hasan, M.S. & Yu, H. (2015) Innovative developments in HCI and future trends. *21st International Conference on Automation and Computing (ICAC)*, pp. 1-6. IEEE.

Hawkins, B.A., Diniz-Filho, F. & Alexandre, J. (2004) 'Latitude'and geographic patterns in species richness. *Ecography,* **27,** 268-272.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T. & O'Brien, E.M. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology,* **84,** 3105-3117.

Hawkins, B.A., Porter, E.E., Diniz-Filho, F. & Alexandre, J. (2003) Productivity and

history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84,** 1608-1623.

Haynie, D.T. (2007) And the Award goes to…. *International Journal of Nanomedicine*, **2,** 125.

Heidorn, P.B. (2008) Shedding light on the dark data in the long tail of science. *Library Trends*, **57,** 280-299.

Higgs, E. (2003) *Nature by Design: People, Natural Process, and Ecological Restoration.* MIT Press, Boston.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163,** 192-211.

Hillebrand, H. & Gurevitch, J. (2013) Reporting standards in experimental studies. *Ecology Letters*, **16,** 1419-1420.

Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24,** 599-605.

Hodgson, M.E. & Bresnahan, P. (2004) Accuracy of airborne lidar-derived elevation. *Photogrammetric Engineering & Remote Sensing*, **70,** 331-339.

Hogeweg, P. (1988) Cellular automata as a paradigm for ecological modeling. *Applied Mathematics and Computation*, **27,** 81-100.

Hu, J. (1995) Methods of generating surfaces in environmental GIS applications. *1995 ESRI User Conference Proceedings*.

Hughes, T.P., Gunderson, L.H., Folke, C., Baird, A.H., Bellwood, D., Berkes, F., Crona, B., Helfgott, A., Leslie, H. & Norberg, J. (2007) Adaptive management of the great barrier reef and the Grand Canyon world heritage areas. *Ambio*, **36,** 586-592.

Hui, C., Veldtman, R. & McGeoch, M.A. (2010) Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, **33,** 95-102.

Hunter, J.R., Craig, P.D. & Phillips, H.E. (1993) On the use of random walk models with spatially variable diffusivity. *Journal of Computational Physics*, **106,**

366-376.

Illian, J.B., Martino, S., Sørbye, S.H., Gallego-Fernández, J.B., Zunzunegui, M., Esquivias, M.P. & Travis, J.M. (2013) Fitting complex ecological point process models with integrated nested Laplace approximation. *Methods in Ecology and Evolution,* **4,** 305-315.

Illian, J.B., Møller, J. & Waagepetersen, R.P. (2009) Hierarchical spatial point process analysis for a plant community with high biodiversity. *Environmental and Ecological Statistics,* **16,** 389-405.

Ioannidis, J.P.A., Fanelli, D., Dunne, D.D. & Goodman, S.N. (2015) Meta-research: evaluation and improvement of research methods and practices. *PLoS Biology,* **13,** e1002264.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science,* **314,** 102-106.

James, T.D., Murray, T., Barrand, N.E. & Barr, S.L. (2006) Extracting photogrammetric ground control from LiDAR DEMs for change detection. *The Photogrammetric Record,* **21,** 312-328.

Jonsson, B.G. (2000) Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science,* **11,** 51-56.

Jonsson, B.G. & Dynesius, M. (1993) Uprooting in boreal spruce forests - long-term variation in disturbance rate. *Canadian Journal of Forest Research,* **23,** 2383-2388.

Josefsson, T., Hornberg, G. & Ostlund, L. (2009) Long-term human impact and vegetation changes in a boreal forest reserve: implications for the use of protected areas as ecological references. *Ecosystems,* **12,** 1017-1036.

Karafyllidis, I. & Thanailakis, A. (1997) A model for predicting forest fire spreading using cellular automata. *Ecological Modelling,* **99,** 87-97.

Keddy, P.A. (1994) Applications of the Hertzsprung-Russell star chart to ecology: reflections on the 21st birthday of Geographical Ecology. *Trends in Ecology &*

Evolution, **9,** 231-234.

Keller, E.A. & Swanson, F.J. (1979) Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes,* **4,** 361-380.

Keylock, C.J. (2005) Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos,* **109,** 203-207.

Kimiko, R. & Alice, A. (2013) Off the paved paths: exploring nature with a mobile augmented reality learning tool. *International Journal of Mobile Human Computer Interaction (IJMHCI),* **5,** 21-49.

Kirby, K.J., Reid, C.M., Thomas, R.C. & Goldsmith, F.B. (1998) Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology,* **35,** 148-155.

Laiho, R. & Prescott, C.E. (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forest Research,* **34,** 763-777.

Lande, R., Engen, S. & Saether, B.-E. (2003) *Stochastic Population Dynamics in Ecology and Conservation.* Oxford University Press, London.

Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A., Swanson, F.J., HilleRisLambers, J., Sprugel, D.G. & Franklin, J.F. (2015) Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology,* **11,** 2855-2861.

Larson, L.R., Green, G.T. & Cordell, H. (2011) Children's Time outdoors: results and implications of the national kids survey. *Journal of Park and Recreation Administration,* **29,** 1-20.

Lassueur, T., Joost, S. & Randin, C.F. (2006) Very high resolution digital elevation models: Do they improve models of plant species distribution? *Ecological Modelling,* **198,** 139-153.

Lawes, M.J., Murphy, B.P., Midgley, J.J. & Russell-Smith, J. (2011) Are the eucalypt and non-eucalypt components of Australian tropical savannas independent? *Oecologia,* **166,** 229-239.

Lazarus, R.J. (2009) Super wicked problems and climate change: restraining the present to liberate the future. *Cornell Law Review*, **94,** 1153-1234.

Ledo, A. (2015) Protocol for inventory of mapped plots in tropical forest. *Journal of Tropical Forest Science*, **27,** 240-247.

Lehmann, S. & Huth, A. (2015) Fast calibration of a dynamic vegetation model with minimum observation data. *Ecological Modelling*, **301,** 98-105.

Levick, S.R. & Asner, G.P. (2013) The rate and spatial pattern of treefall in a savanna landscape. *Biological Conservation*, **157,** 121-127.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73,** 1943-1967.

Li, L., Huang, Z., Ye, W., Cao, H., Wei, S., Wang, Z., Lian, J., Sun, I.F., Ma, K. & He, F. (2009) Spatial distributions of tree species in a subtropical forest of China. *Oikos*, **118,** 495-502.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. (1985) Mortality patterns and stand turnover rates in a wet tropical forest in costa rica. *Journal of Ecology*, **73,** 915-924.

Liedloff, A.C. & Cook, G.D. (2007) Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the FLAMES simulation model. *Ecological Modelling*, **201,** 269-282.

Lindenmayer, D.B. & Franklin, J.F. (2002) *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach.* Island Press, New York.

Linn, R.R., Winterkamp, J.L., Weise, D.R. & Edminster, C. (2010) A numerical study of slope and fuel structure effects on coupled wildfire behaviour. *International Journal of Wildland Fire*, **19,** 179-201.

Liu, X. (2008) Airborne LiDAR for DEM generation: some critical issues. *Progress in Physical Geography*, **32,** 31-49.

Liu, X., Zhang, Z., Peterson, J. & Chandra, S. (2007) LiDAR-derived high quality ground control information and DEM for image orthorectification.

GeoInformatica, **11,** 37-53.

Loeb, A. (2016) Good data are not enough. *Nature,* **539,** 23-25.

Lorimer, C.G. (1985) Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research,* **15,** 200-213.

Lorrey, A. & Martin, T. (2005) Use of modern tree-fall patterns as a guideline for interpreting prostrate trees at a pre–Last Glacial Maximum paleoforest site, upper North Island, New Zealand. *Journal of Geophysical Research: Biogeosciences,* **110**.

Lugo, A.E. & Scatena, F.N. (1996) Background and catastrophic tree mortality in tropical moist, wet, and rain rorests. *Biotropica,* **28,** 585-599.

Lund, H.G. (2002) When is a forest not a forest? *Journal of Forestry,* **100,** 21-28.

Macal, C.M. & North, M.J. (2010) Tutorial on agent-based modelling and simulation. *Journal of Simulation,* **4,** 151-162.

Manfredo, M.J., Teel, T.L. & Dietsch, A.M. (2016) Implications of human value shift and persistence for biodiversity conservation. *Conservation Biology,* **30,** 287-296.

Mannion, P.D., Upchurch, P., Benson, R.B. & Goswami, A. (2014) The latitudinal biodiversity gradient through deep time. *Trends in Ecology & Evolution,* **29,** 42-50.

Marris, E. (2011) *The Rambunctious Garden: Saving Nature in a Post-Wild World.* Bloomsbury, New York.

Martin, H. (2006) Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of Arid Environments,* **66,** 533-563.

Maser, C. (1984) The seen and unseen world of the fallen tree. *General Technical Report, Pacific Northwest Forest and Range Experiment Station, USDA Forest Service***,** ii + 56pp.-ii + 56pp.

May, F., Huth, A. & Wiegand, T. (2015) Moving beyond abundance distributions: neutral theory and spatial patterns in a tropical forest. *Proceedings of the Royal*

Society of London B: Biological Sciences, **282,** 20141657.

May, F., Wiegand, T., Lehmann, S. & Huth, A. (2016) Do abundance distributions and species aggregation correctly predict macroecological biodiversity patterns in tropical forests? *Global Ecology and Biogeography*.

McCarthy, B.C. & Bailey, R.R. (1994) Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. *Canadian Journal of Forest Research,* **24,** 1317-1329.

McGlade, J. (2009) *Advanced Ecological Theory: Principles and Applications.* John Wiley & Sons, New Jersey.

McIntire, E.J.B. & Fajardo, A. (2009) Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology,* **90,** 46-56.

Metzger, N. & Zare, R.N. (1999) Interdisciplinary research: From belief to reality. *Science,* **283,** 642-643.

Meyfroidt, P., Rudel, T.K. & Lambin, E.F. (2010) Forest transitions, trade, and the global displacement of land use. *Proceedings of the National Academy of Sciences of the United States of America,* **107,** 20917-22.

Mitchard, E.T., Saatchi, S.S., White, L., Abernethy, K., Jeffery, K.J., Lewis, S.L., Collins, M., Lefsky, M.A., Leal, M.E. & Woodhouse, I.H. (2012) Mapping tropical forest biomass with radar and spaceborne LiDAR in Lopé National Park, Gabon: overcoming problems of high biomass and persistent cloud. *Biogeosciences,* **9,** 179-191.

Moeur, M. (1997) Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla*/*Thuja plicata* forests. *Forest Ecology and Management,* **94,** 175-186.

Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, **14,** 1211-1219.

Moser, K., Ahn, C. & Noe, G. (2007) Characterization of microtopography and its

influence on vegetation patterns in created wetlands. *Wetlands,* **27,** 1081-1097.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., Van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M. & Kram, T. (2010) The next generation of scenarios for climate change research and assessment. *Nature,* **463,** 747-756.

Mücke, W., Deák, B., Schroiff, A., Hollaus, M. & Pfeifer, N. (2013) Detection of fallen trees in forested areas using small footprint airborne laser scanning data. *Canadian Journal of Remote Sensing,* **39,** S32-S40.

Muir, P.S. (1993) Disturbance effects on structure and tree species composition of *Pinus contorta* forests in western Montana. *Canadian Journal of Forest Research,* **23,** 1617-1625.

Müller, J. & Bütler, R. (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research,* **129,** 981-992.

Murrell, D.J. (2009) On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? *Journal of Ecology,* **97,** 256-266.

Murrell, D.J., Purves, D.W. & Law, R. (2001) Uniting pattern and process in plant ecology. *Trends in Ecology & Evolution,* **16,** 529-530.

Muscolo, A., Bagnato, S., Sidari, M. & Mercurio, R. (2014) A review of the roles of forest canopy gaps. *Journal of Forestry Research,* **25,** 725-736.

Nagalingum, N.S., Knerr, N., Laffan, S.W., González-Orozco, C.E., Thornhill, A.H., Miller, J.T. & Mishler, B.D. (2015) Continental scale patterns and predictors of fern richness and phylogenetic diversity. *Frontiers in Genetics,* **6,** 132.

Nakagawa, Y., Yokozawa, M. & Hara, T. (2015) Competition among plants can lead to an increase in aggregation of smaller plants around larger ones. *Ecological Modelling*, **301,** 41-53.

Nakamaru, M. (2006) Lattice models in ecology and social sciences. *Ecological*

Research, **21,** 364-369.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W. & Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature,* **520,** 45-50.

Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S. & Crowston, K. (2012) The future of citizen science: emerging technologies and shifting paradigms. *Frontiers in Ecology and the Environment,* **10,** 298-304.

Noss, R.F. (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. *Forest Ecology and Management,* **115,** 135-146.

Nunes, M.d.O. & Mayer, V.F. (2014) Mobile technology, games and nature areas: The tourist perspective. *Tourism & Management Studies,* **10,** 53-58.

Oberle, B., Milo, A., Myers, J.A., Young, D.F., Walton, M.L. & Zanne, A.E. (2015) Direct estimates of downslope deadwood movement over 30 years in a temperature forest illustrate impacts of treefall on forest ecosystem dynamics. *Canadian Journal of Forest Research*.

Odobasic, D., Medak, D. & Miler, M. (2013) Gamification of geographic data collection. *Gi_Forum 2013: Creating the Gisociety,* 328-337.

Oliver, T.H. & Morecroft, M.D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change,* **5,** 317-335.

O'Loughlin, F.E., Paiva, R.C.D., Durand, M., Alsdorf, D.E. & Bates, P.D. (2016) A multi-sensor approach towards a global vegetation corrected SRTM DEM product. *Remote Sensing of Environment,* **182,** 49-59.

Ondei, S., Prior, L.D., Vigilante, T. & Bowman, D.M.J.S. (2016) Post-fire resprouting strategies of rainforest and savanna saplings along the rainforest–savanna boundary in the Australian monsoon tropics. *Plant Ecology*, **217,** 711-724.

O'Neill, R.V., Riitters, K.H., Wickham, J. & Jones, K.B. (1999) Landscape pattern metrics and regional assessment. *Ecosystem Health,* **5,** 225-233.

Orwin, K.H., Wardle, D.A., Greenfield, L.G., Set, xe, xe & Heikki (2006) Context-dependent changes in the resistance and resilience of soil microbes to an experimental distrubance for three primary plant chronosequences. *Oikos,* **112,** 196-208.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011) A large and persistent carbon sink in the world's forests. *Science*, **333,** 988-993.

Pan, Y., Birdsey, R.A., Phillips, O.L. & Jackson, R.B. (2013) The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics,* **44,** 593-622.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20,** 170-180.

Pärtel, M., Bennett, J.A. & Zobel, M. (2016) Macroecology of biodiversity: disentangling local and regional effects. *New Phytologist,* **211,** 404-410.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C. & Fasth, B. (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, **315,** 361-364.

Pasher, J. & King, D.J. (2009) Mapping dead wood distribution in a temperate hardwood forest using high resolution airborne imagery. *Forest Ecology and Management,* **258,** 1536-1548.

Pearson, D.M. (2002) The application of local measures of spatial autocorrelation for describing pattern in north Australian landscapes. *Journal of Environmental*

Management, **64,** 85-95.

Peck, S.L. (2004) Simulation as experiment: a philosophical reassessment for biological modeling. *Trends in Ecology & Evolution,* **19,** 530-534.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F. & Evengård, B. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science,* **355,** eaai9214.

Perry, G.L., Miller, B.P., Lamont, B.B. & Enright, N.J. (2017) Community-level spatial structure supports a model of stochastic geometry in species-rich shrublands. *Oikos,* **126,** 833-842.

Perry, G.L.W., Enright, N., Miller, B. & Lamont, B. (2008) Spatial patterns in species-rich sclerophyll shrublands of southwestern Australia. *Journal of Vegetation Science,* **19,** 705-716.

Perry, G.L.W., Enright, N.J., Miller, B.P. & Lamont, B.B. (2013) Do plant functional traits determine spatial pattern? A test on species-rich shrublands, Western Australia. *Journal of Vegetation Science,* **24,** 441-452.

Perry, J.N., Liebhold, A.M., Rosenberg, M.S., Dungan, J., Miriti, M., Jakomulska, A. & Citron-Pousty, S. (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography,* **25,** 578-600.

Perz, S.G. (2007) Grand theory and context-specificity in the study of forest dynamics: forest transition theory and other directions. *The Professional Geographer,* **59,** 105-114.

Peterson, C.J., Carson, W.P., McCarthy, B.C. & Pickett, S.T.A. (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos,* **58,** 39-46.

Peterson, C.J. & Pickett, S.T.A. (1991) Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. *Forest Ecology and Management,* **42,** 205-217.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist,* **100,** 33-46.

Pielou, E. (1960) A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology***,** 575-584.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science,* **344**.

Pimm, S.L. & Raven, P. (2000) Biodiversity: extinction by numbers. *Nature,* **403,** 843-845.

Plotkin, J., Chave, J. & Ashton, P.S. (2002) Cluster analysis of spatial patterns in Malaysian tree species. *American Naturalist,* **160,** 629-644.

Powell, M.G. & Glazier, D.S. (2017) Asymmetric geographic range expansion explains the latitudinal diversity gradients of four major taxa of marine plankton. *Paleobiology,* **43,** 196-208.

Prescott, C. (2002) The influence of the forest canopy on nutrient cycling. *Tree Physiology,* **22,** 1193-1200.

Putz, F.E. & Redford, K.H. (2010) The Importance of defining 'forest': tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica,* **42,** 10-20.

Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science,* **12,** 553-566.

Qian, H., Badgley, C. & Fox, D.L. (2009) The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography,* **18,** 111-122.

R Core Team (2017) R: A Language and Environment for Statistical Computing, v3.4 (r-project.org). *R Foundation for Statistical Computing*. Vienna, Austria.

Rademacher, C., Neuert, C., Grundmann, V., Wissel, C. & Grimm, V. (2004)

Reconstructing spatiotemporal dynamics of Central European natural beech forests: the rule-based forest model BEFORE. *Forest Ecology and Management,* **194,** 349-368.

Railsback, S.F. & Grimm, V. (2011) *Agent-Based and Individual-Based Modeling: A Practical Ontroduction.* Princeton University Press, New Jersey.

Reich, P.B., Luo, Y., Bradford, J.B., Poorter, H., Perry, C.H. & Oleksyn, J. (2014) Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences of the United States of America,* **111,** 13721-13726.

Reichman, O.J., Jones, M.B. & Schildhauer, M.P. (2011) Challenges and opportunities of open data in ecology. *Science,* **331,** 703-705.

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J., Vanderwel, M.C., Verbeeck, H. & Villela, D.M. (2015) Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *Journal of Ecology,* **103,** 5-15.

Rhoten, D. & Parker, A. (2004) Risks and rewards of an interdisciplinary research path. *Science,* **306,** 2046.

Rich, R.L., Frelich, L.E. & Reich, P.B. (2007) Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. *Journal of Ecology*, **95,** 1261-1273.

Richerzhagen, B., Stingl, D., Hans, R., Gross, C. & Steinmetz, R. (2014) Bypassing the cloud: Peer-assisted event dissemination for augmented reality games. *14th IEEE International Conference on Peer-to-Peer Computing*, pp. 1-10.

Rogers, P. (1996) *Disturbance Ecology and Forest Management: A Review of the Literature.* US Department of Agriculture, Forest Service, Intermountain Research Station Ogden, Utah.

Rohde, K. (1999) Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the

gradients? *Ecography,* **22,** 593-613.

Rosenfield, P.L. (1992) The potential of transdisciplinary research for sustaining and extending linkages between the health and social sciences. *Social Science & Medicine,* **35,** 1343-1357.

Rouvinen, S. & Kuuluvainen, T. (2001) Amount and spatial distribution of standing and downed dead trees in two areas of different fire history in a boreal scots pine forest. *Ecological Bulletins,* **49,** 115-127.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P. & Senock, R.S. (2004) An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs,* **74,** 393-414.

Šamonil, P., Král, K. & Hort, L. (2010) The role of tree uprooting in soil formation: A critical literature review. *Geoderma,* **157,** 65-79.

Schliemann, S.A. & Bockheim, J.G. (2011) Methods for studying treefall gaps: A review. *Forest Ecology and Management,* **261,** 1143-1151.

Schmitt, C.B., Burgess, N.D., Coad, L., Belokurov, A., Besançon, C., Boisrobert, L., Campbell, A., Fish, L., Gliddon, D. & Humphries, K. (2009) Global analysis of the protection status of the world's forests. *Biological Conservation,* **142,** 2122-2130.

Schumann, G., Matgen, P., Cutler, M.E.J., Black, A., Hoffmann, L. & Pfister, L. (2008) Comparison of remotely sensed water stages from LiDAR, topographic contours and SRTM. *ISPRS Journal of Photogrammetry and Remote Sensing,* **63,** 283-296.

Seibert, J., Stendahl, J. & Sorensen, R. (2007) Topographical influences on soil properties in boreal forests. *Geoderma,* **141,** 139-148.

Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology,* **4,** e344.

Sharma, J. & Sharma, Y. (2004) Nutrient cycling in forest ecosystems - A review. *Agricultural Reviews,* **25,** 157-172.

Shen, G., He, F., Waagepetersen, R., Sun, I.-F., Hao, Z., Chen, Z.-S. & Yu, M. (2013) Quantifying effects of habitat heterogeneity and other clustering processes on spatial distributions of tree species. *Ecology,* **94,** 2436-2443.

Sheng, L.Y. (2013) Modelling learning from Ingress (Google's augmented reality social game). *IEEE 63rd Annual Conference International Council for Education Media,* pp. 1-8. Singapore.

Shifley, S.R., He, H.S., Lischke, H., Wang, W.J., Jin, W., Gustafson, E.J., Thompson, J.R., Thompson, F.R., Dijak, W.D. & Yang, J. (2017) The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. *Landscape Ecology***,** doi: 10.1007/s10980-017-0540-9.

Siegert, F., Ruecker, G., Hinrichs, A. & Hoffmann, A.A. (2001) Increased damage from fires in logged forests during droughts caused by El Nino. *Nature,* **414,** 437-440.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins***,** 11-41.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management,* **128,** 211-225.

Silvertown, J. (2009) A new dawn for citizen science. *Trends in Ecology & Evolution,* **24,** 467-471.

Sobhani, V.M., Barrett, M. & Peterson, C.J. (2014) Robust prediction of treefall pit and mound sizes from tree size across 10 forest blowdowns in eastern North America. *Ecosystems,* **17,** 837-850.

Soderberg, U., Wulff, S. & Stahl, G. (2014) The choice of definition has a large effect on reported quantities of dead wood in boreal forest. *Scandinavian Journal of Forest Research,* **29,** 252-258.

Sollins, P. (1982) Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research,* **12,** 18-28.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D. & Spycher, G. (1987) Patterns of log decay in old-growth Douglas-fir forests. *Canadian Journal of Forest Research,* **17,** 1585-1595.

Spano, C.A., Hernández, C.E. & Rivadeneira, M.M. (2015) Evolutionary dispersal drives the latitudinal diversity gradient of stony corals. *Ecography*.

Spies, T.A. (1998) Forest structure: a key to the ecosystem. *Northwest Science,* **72,** 34-36.

Stachowicz, J.J. (2001) Mutualism, facilitation, and the structure of ecological communities. *BioScience,* **51,** 235-246.

Stirling, G. & Wilsey, B. (2001) Empirical relationships between species richness, evenness, and proportional diversity. *American Naturalist,* **158,** 286-299.

Stoyan, D. & Ohser, J. (1982) Correlations between planar random structures, with an ecological application. *Biometrical Journal,* **24,** 631-647.

Stoyan, D. & Penttinen, A. (2000) Recent applications of point process methods in forestry statistics. *Statistical Science,* **15,** 61-78.

Su, J. & Bork, E. (2006) Influence of vegetation, slope, and LiDAR sampling angle on DEM accuracy. *Photogrammetric Engineering & Remote Sensing,* **72,** 1265-1274.

Swart, J.A., van der Windt, H.J. & Keulartz, J. (2001) Value of nature in conservation and restoration. *Restoration Ecology,* **9,** 230-238.

Swetnam, T.W. (1993) Fire history and climate change in giant sequoia groves. *Science,* **262,** 885-889.

Szwagrzyk, J. & Czerwczak, M. (1993) Spatial Patterns of trees in natural forests of East-Central Europe. *Journal of Vegetation Science,* **4,** 469-476.

Takahashi, D. (2014) *Google's mobile game Ingress enables 7M players to create user-generated missions*, Venture Beats - News, http://venturebeat.com/2014/09/25/googles-mobile-game-ingress-enables-7m-players-to-create-user-generated-missions/.

Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van Der Hout, P., Daly, D.C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., De Oliveira, A.A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., NúÑez Vargas, P., Mogollón, H. & Morawetz, W. (2003) A spatial model of tree α-diversity and tree density for the Amazon. *Biodiversity & Conservation,* **12,** 2255-2277.

Thompson, I., Mackey, B., McNulty, S. & Mosseler, A. (2009) *Forest resilience, biodiversity, and climate change.* Secretariat of the Convention on Biological Diversity, Montreal. Technical Series, Canada.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science,* **294,** 843-845.

Tonini, F., Hochmair, H.H., Scheffrahn, R.H. & DeAngelis, D.L. (2014) Stochastic spread models: a comparison between an individual-based and a lattice-based model for assessing the expansion of invasive termites over a landscape. *Ecological Informatics,* **24,** 222-230.

Torchin, M.E., Miura, O. & Hechinger, R.F. (2015) Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. *Ecology,* **96,** 3033-3042.

Trumbore, S., Brando, P. & Hartmann, H. (2015) Forest health and global change. *Science,* **349,** 814-818.

Truong, M., Prévot, A. & Clayton, S. (2015) Gamers like it green: Virtual Biophilia-like experience in Virtual Universes. *International Congress for Conservation Biology*. Montpellier, France

Uhl, C., Clark, K., Dezzeo, N. & Maquirino, P. (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology,* **69,** 751-763.

Ulanova, N.G. (2000) The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management,* **135,** 155-167.

Valladares, F. & Niinemets, Ü. (2008) Shade tolerance, a key plant feature of complex

nature and consequences. *Annual Review of Ecology, Evolution, and Systematics***,** 237-257.

van der Meer, P.J. & Bongers, F. (1996) Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *Journal of Ecology*, **84,** 19-29.

van der Meer, P.J., Dignan, P. & Saveneh, A.G. (1999) Effect of gap size on seedling establishment, growth and survival at three years in mountain ash (*Eucalyptus regnans* F. Muell.) forest in Victoria, Australia. *Forest Ecology and Management,* **117,** 33-42.

van der Vaart, E., Beaumont, M.A., Johnston, A.S. & Sibly, R.M. (2015) Calibration and evaluation of individual-based models using Approximate Bayesian Computation. *Ecological Modelling,* **312,** 182-190.

van Gemerden, B.S., Olff, H., Parren, M.P.E. & Bongers, F. (2003) The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J Biogeogr,* **30,** 1381-1390.

Vanderwel, M.C., Malcolm, J.R. & Smith, S.M. (2006) An integrated model for snag and downed woody debris decay class transitions. *Forest Ecology and Management,* **234,** 48-59.

Velázquez, E., Martínez, I., Getzin, S., Moloney, K.A. & Wiegand, T. (2016) An evaluation of the state of spatial point pattern analysis in ecology. *Ecography***,** doi:10.1111/ecog.01579.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M. & Trasobares, A. (2013) Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE,* **8,** e53530.

Vlahakis, V., Ioannidis, N., Karigiannis, J., Tsotros, M., Gounaris, M., Stricker, D., Gleue, T., Daehne, P. & Almeida, L. (2002) Archeoguide: An augmented reality guide for archaeological sites. *IEEE Computer Graphics and Applications,* **219,** 52-60.

Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S.J. & Hao, Z. (2011) Spatial

patterns of tree species richness in two temperate forests. *Journal of Ecology*, **99,** 1382-1393.

Wang, X., Ye, J., Li, B., Zhang, J., Lin, F. & Hao, Z. (2010) Spatial distributions of species in an old-growth temperate forest, northeastern China. *Canadian Journal of Forest Research*, **40,** 1011-1019.

Warren, S.D., Hohmann, M.G., Auerswald, K. & Mitasova, H. (2004) An evaluation of methods to determine slope using digital elevation data. *CATENA*, **58,** 215-233.

Webber, B.L., Norton, B.A. & Woodrow, I.E. (2010) Disturbance affects spatial patterning and stand structure of a tropical rainforest tree. *Austral Ecology*, **35,** 423-434.

Weedon, J.T., Cornwell, W.K., Cornelissen, J.H., Zanne, A.E., Wirth, C. & Coomes, D.A. (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters*, **12,** 45-56.

West, D.C., Shugart, H.H. & Botkin, D. (2012) *Forest Succession: Concepts and Application.* Springer Science & Business Media, New York.

Whitmore, T. (1989) Canopy gaps and the two major groups of forest trees. *Ecology*, **70,** 536-538.

Wiegand, K., Jeltsch, F. & Ward, D. (2000) Do spatial effects play a role in the spatial distribution of desert-dwelling *Acacia raddiana*? *Journal of Vegetation Science*, **11,** 473-484.

Wiegand, T., Gunatilleke, S. & Gunatilleke, N. (2007) Species associations in a heterogeneous Sri Lankan dipterocarp forest. *American Naturalist*, **170,** E77-E95.

Wiegand, T., Jeltsch, F., Hanski, I. & Grimm, V. (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos*, **100,** 209-222.

Wiegand, T. & Moloney, K.A. (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, **104,** 209-229.

Wiegand, T. & Moloney, K.A. (2013) *Handbook of Spatial Point-Pattern Analysis in Ecology*. CRC Press, Boca Raton, Florida.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3,** 385-397.

Wiens, J.A. (2007) *Foundation Papers in Landscape Ecology*. Columbia University Press, New York.

Willig, M.R., Kaufman, D. & Stevens, R. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34,** 273-309.

Wilson, E.O. (2007) Biophilia and the conservation ethic. *Evolutionary Perspectives on Environmental Problems* (eds D.J. Pen & I. Mysterud), pp. 249-257. Transactions Publishers, USA.

Wing, B.M., Ritchie, M.W., Boston, K., Cohen, W.B., Gitelman, A. & Olsen, M.J. (2012) Prediction of understory vegetation cover with airborne lidar in an interior ponderosa pine forest. *Remote Sensing of Environment*, **124,** 730-741.

Woldendorp, G. & Keenan, R.J. (2005) Coarse woody debris in Australian forest ecosystems: a review. *Austral Ecology*, **30,** 834-843.

Wood, S.W., Murphy, B.P. & Bowman, D.M.J.S. (2011) Firescape ecology: how topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area. *J Biogeogr*, **38,** 1807-1820.

Wood, S.W., Prior, L.D., Stephens, H.C. & Bowman, D.M. (2015) Macroecology of Australian tall eucalypt forests: baseline data from a continental-scale permanent plot network. *PLoS ONE*, **10,** e0137811.

Yin, Z.-Y. & Wang, X. (1999) A cross-scale comparison of drainage basin characteristics derived from digital elevation models. *Earth Surface Processes and Landforms*, **24,** 557-562.

You, H., He, D., You, W., Xiao, S., Hong, W. & Ieee (2012) Spatial distribution pattern of coarse woody debris (CWD) in two typical forest types in Tianbaoyan

National Nature Reserve. *2012 World Automation Congress (Wac)*.

Zanne, A.E., Oberle, B., Dunham, K.M., Milo, A.M., Walton, M.L. & Young, D.F. (2015) A deteriorating state of affairs: How endogenous and exogenous factors determine plant decay rates. *Journal of Ecology*, **103,** 1421-1431.

Zellweger, F., Morsdorf, F., Purves, R.S., Braunisch, V. & Bollmann, K. (2014) Improved methods for measuring forest landscape structure: LiDAR complements field-based habitat assessment. *Biodiversity & Conservation*, **23,** 289-307.

Zhang, X., Drake, N.A., Wainwright, J. & Mulligan, M. (1999) Comparison of slope estimates from low resolution DEMs: Scaling issues and a fractal method for their solution. *Earth Surface Processes and Landforms*, **24,** 763-779.

Zhang, Z., Hu, G., Zhu, J. & Ni, J. (2012) Aggregated spatial distributions of species in a subtropical karst forest, southwestern China. *Journal of Plant Ecology*, **6,** 131-140.

Zhou, L., Dai, L.-m., Gu, H.-y. & Zhong, L. (2007) Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. *Journal of Forestry Research*, **18,** 48-54.

Zhu, J., Lu, D. & Zhang, W. (2014) Effects of gaps on regeneration of woody plants: a meta-analysis. *Journal of Forestry Research*, **25,** 501-510.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18,** 1042-1052.

Ziadat, F.M. (2007) Effect of contour intervals and grid cell size on the accuracy of DEMs and slope derivatives. *Transactions in GIS*, **11,** 67-81.

Zielonka, T. (2006) When does dead wood turn into a substrate for spruce replacement? *Journal of Vegetation Science*, **17,** 739-746.

SUPPLEMENTARY MATERIAL

Supplementary material is provided at the end of this thesis for the following chapters:

Appendix 1: Chapter II: A GLOBAL SYNTHESIS OF REPORTED SPATIAL PATTERNS IN FORESTS

Appendix 2: Chapter IV: LATITUDINAL CONTROLS ON FOREST SPECIES RICHNESS ARE NOT DIRECT

Appendix 3: Chapter V: LOOK DOWN TO SEE WHAT'S UP: A SYSTEMATIC OVERVIEW OF TREEFALL DYNAMICS IN FORESTS

Appendix 4: Chapter VI: READING THE FOREST LOGBOOK: ENVIRONMENTAL DRIVERS OF LIVING AND DEAD ELEMENTS OF AUSTRALIAN EUCALYPT FORESTS

Appendix 5: Chapter VIII: A PRACTICAL METHOD FOR CREATING A DIGITAL TOPOGRAPHIC SURFACE FOR ECOLOGICAL PLOTS USING GROUND-BASED MEASUREMENTS

Appendix 6: Chapter IX: MODELLING LINEAR SPATIAL FEATURES IN ECOLOGY

Appendix 1

Chapter II: A GLOBAL SYNTHESIS OF REPORTED SPATIAL PATTERNS IN FORESTS

Supplementary Methods

Appendix 1a: Selection and exclusion criteria for studies

After initial database queries (as described in Methods section of the main paper), we undertook a further series of interrogation of the peer-reviewed literature in order to ensure we had collected a comprehensive representation of studies. The following approaches were used:

a) The reference lists from recent highly cited manuscripts in the field, and the subsequent citations of these papers, were checked.
b) The citation list of *Programita* (a well-known statistical software package that analyses spatial point-pattern data) was searched (http://programita.org/).
c) We crosschecked the literature pre-2000 (which typically used quadrat-count methods, before advancements of metrics such as Ripley's K), to ensure that year of publication did not bias in our selection protocol.

The search criteria for pattern information in global forest plots was relatively general, resulting in ~12,000 papers being uncovered. However, it is often the case that papers might be relevant (i.e., report spatial pattern statistics and analyses) despite not having 'pattern' appearing anywhere in the title or abstract. We accounted for this potential selection bias by using the broader search methods described above.

The criteria against which we selected (or excluded) the global forest plot studies were strict. The papers had to meet the following conditions:

a) Full-text of the paper was available (and in English)
b) Used regular-shaped plots within which data were collected (i.e., square/rectangular)

c) Had the primary aim of analysing and characterising the spatial pattern (rather than used for model comparisons, etc.)
d) The pattern information was mentioned explicitly in the text, or represented as a table or in graph form. Summarized information (e.g., “20% of the plots studied were aggregated” was insufficient).
e) Explicit geographic co-ordinates for each plot were reported (i.e., each plot needed to be treated as separable unit).

Final list of papers that reported data useable for a quantitative synthesis, and were thus included in the database, are cited at the end of this supplementary material.

Appendix 1b: Pattern as a categorical variable

We chose to classify pattern as a categorical variable rather than a raw numerical (continuous) value, because of substantial study-by-study variation (and inconsistency) in the following:

a) The methods used to classify pattern information (e.g., PCF vs. Ripley’s *K* or *L*).
b) The magnitude of the summary statistic (ranged from 1.4 - 60) when graphs were presented. This wide scale of reported values would have made comparisons between summary statistics difficult to standardise, and would have greatly reduced the sample size of papers (though we do acknowledge that the large scale is, in part, because Ripley’s *K* is not density corrected, whereas PCF is. Including their cumulative and non-cumulative nature)
c) Whether confidence intervals and Monte Carlo simulations were derived and reported
d) The distances across which the observed pattern-type were analyzed
e) The quality of the plot images (legibility, font sizes, different scaled axes)

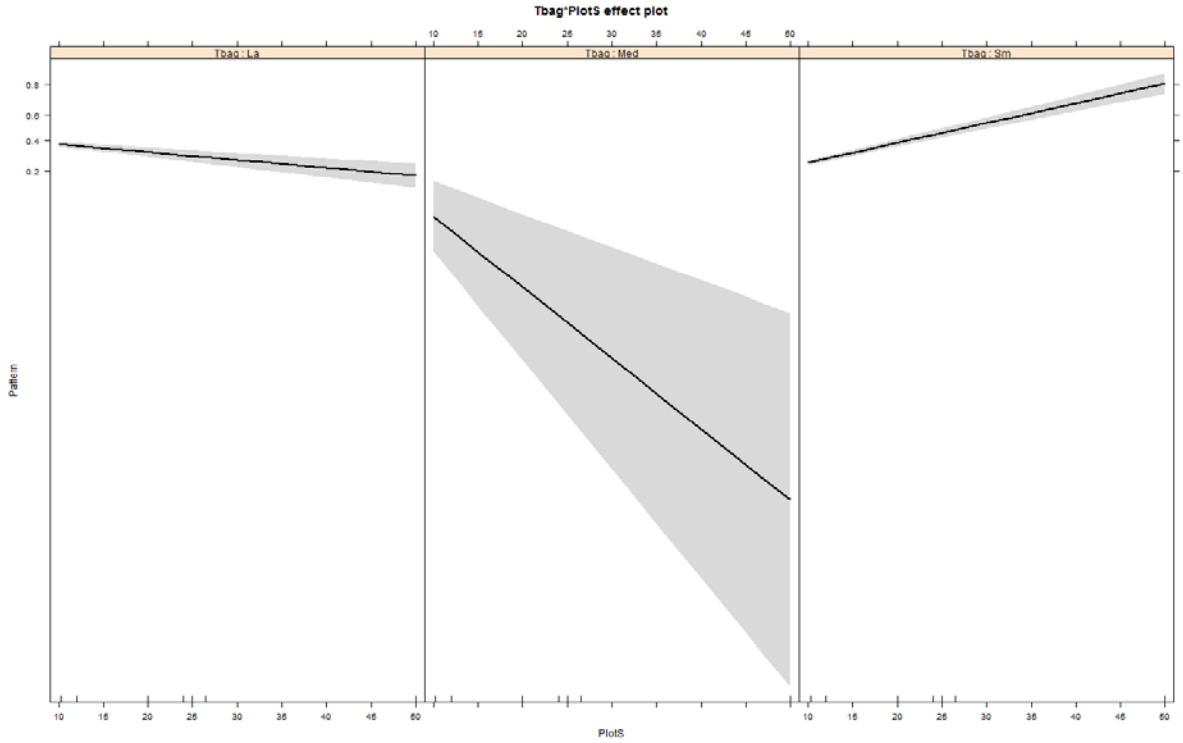
Although we were unable to classify across papers based on the nature of any aggregation (i.e., first-order versus second-order aggregation [which was variably evaluated by appropriate nulls among studies]), our decision to use a categorical variable for pattern-type description allowed for direct comparisons among a larger sample size of papers reporting the 'general' spatial pattern. This pragmatic choice permitted the collation and cross-comparisons of a more statistically robust and representative suite of comparison studies.

Appendix 1c: Tree-size measured as a categorical variable

The size of tree measured (diameter at breast height, in centimetres) was highly variable across studies. We pooled these data into small (>1, >1.3, >1.5, >2 and >2.5 cm) and large (>10, >15 and >30 cm) bins, because we wanted to test the two 'extremes' and tease out any broad effects. We tested the sensitivity in our bin-size classification of tree-size measured, by doing a separate analysis on a reduced dataset based only >1 cm and >10 cm tree sizes measured; this revealed nearly identical results to our 'pooled' small and large classifications.

Additionally, there were studies that used 'intermediate' (or medium) minimum tree size measured (>4 cm to >7.5 cm). These were excluded from the primary analyses because of small sample sizes, which led to large error bars in the slope of the effects plots (as illustrated below).

Fig. A1. Effect of interaction between tree size measured (Tbag, categorical: large, medium and small) and plot size measured (PlotS: continuous) on frequency of reported aggregation in global forest plots.



We also note that it is often not common practice in published studies to measure trees starting at intermediate size classes – small sizes (<1 cm to <2.5 cm) and large sizes (>10 cm to >30 cm) are the typical choice.

Appendix 1d: Sub-analysis of community abundance and density

A sub-analysis of community abundance information (available for 62 plots) revealed a strong relationship between tree density, plot size, minimum tree-size measured and the interaction of these predictors. The best-supported GLM (the saturated model) explained 42.9% of the structural deviance in tree density. The most important single predictor was minimum tree size measured: AIC_c weight $(w_i)_{(\text{size measured})} = 0.988$, $w_{(\text{plot size})} = 0.122$, $w_{(\text{null model})} = 0.00005$. Thus, the evidence ratio of AIC_c weights showed that a minimum size measured model was 80.6 times better supported by the data than plot size. Even though we could not use abundance at

the individual species level (this information was rarely reported), we were able to reveal a strong influence of choice of plot size and tree size measured on prevalence of aggregation.

In addition, the size-threshold for trees to be measured was strongly linked to plot density, with higher densities reported when smaller tree-size classes were included in the point-pattern data for communities.

Appendix 1f: Supplementary References (the 87 papers used in the analysis)

Akhavan, R. et al. 2012. Spatial patterns in different forest development stages of an intact old-growth Oriental beech forest in the Caspian region of Iran. — European Journal of Forest Research 131: 1355-1366.

Aldrich, P. R. et al. 2003. Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession. — Forest Ecology and Management 180: 475-491.

Allen, M. et al. 2012. Windstorm damage and forest recovery: accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests. — Plant Ecology 213: 1833-1842.

Arévalo, J. and Fernández-Palacios, J. 2003. Spatial patterns of trees and juveniles in a laurel forest of Tenerife, Canary Islands. — Plant Ecology 165: 1-10.

Armesto, J. J. et al. 1986. A Comparison of Spatial Patterns of Trees in Some Tropical and Temperate Forests. — Biotropica 18: 1-11.

Bagchi, R. et al. 2011. Spatial patterns reveal negative density dependence and habitat associations in tropical trees. — Ecology 92: 1723-1729.

Batista, J. L. F. and Maguire, D. A. 1998. Modeling the spatial structure of topical forests. — Forest Ecology and Management 110: 293-314.

Beland, M. et al. 2003. Structure, spatial distribution and competition in mixed jack pine (Pines banksiana) stands on clay soils of eastern Canada. — Annals of Forest Science 60: 609-617.

Burns, S. L. et al. 2013. Stand dynamics, spatial pattern and site quality in Austrocedrus chilensis forests in Patagonia, Argentina. — Forest System 22:

Camarero, J. J. et al. 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. — Forest Ecology and Management 134: 1-16.

Carrer, M. et al. 2013. Convergent space–time tree regeneration patterns along an elevation gradient at high altitude in the Alps. — Forest Ecology and Management 304: 1-9.

Chen, J. Q. and Bradshaw, G. A. 1999. Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. — Forest Ecology and Management 120: 219-233.

Cheng, X. et al. 2014. Point pattern analysis of different life stages of Quercus liaotungensis in Lingkong Mountain, Shanxi Province, China. — Journal of Plant Interactions 9: 233-240.

Chu, G. et al. 2014. Spatial patterns and associations of dominant woody species in desert-oasis ecotone of South Junggar Basin, NW China. — Journal of Plant Interactions 9: 738-744.

Couteron, P. and Kokou, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. — Plant Ecology 132: 211-227.

Dagley, C. M. 2008. Spatial pattern of coast redwood in three alluvial flat old-growth forests in northern California. — Forest Science 54: 294-302.

Dimov, L. et al. 2013. Tree species exhibit complex patterns of distribution in bottomland hardwood forests. — Annals of Forest Science 70: 813-823.

Dounavi, A. et al. 2010. Spatial patterns and genetic structures within beech populations (Fagus sylvatica L.) of forked and non-forked individuals. — European Journal of Forest Research 129: 1191-1202.

Druckenbrod, D. L. et al. 2005. Spatial pattern and process in forest stands within the Virginia piedmont. — Journal of Vegetation Science 16: 37-48.

Eichhorn, M. P. 2010. Boreal Forests of Kamchatka: Structure and Composition. — Forests 1: 154-176.

Fajardo, A. and González, M. E. 2009. Replacement patterns and species coexistence in an Andean Araucaria-Nothofagus forest. — Journal of Vegetation Science 20: 1176-1190.

Fajardo, A. et al. 2006. Spatial patterns of regeneration in managed uneven-aged ponderosa pine Douglas-fir forests of Western Montana, USA. — Forest Ecology and Management 223: 255-266.

Fajardo, A. and McIntire, E. J. B. 2010. Merged trees in second-growth, fire-origin forests in Patagonia, Chile: Positive spatial association patterns and their ecological implications. — American Journal of Botany 97: 1424-1430.

Fonton, N. H. et al. 2012. Spatial distributions and interactions of trees in Sudanian woodlands: implications for forest enrichment. — Biotechnologie Agronomie Societe Et Environnement 16: 429-440.

Forget, P. M. et al. 1999. Spatial patterns of two rodent-dispersed rain forest trees Carapa procera (Meliaceae) and Vouacapoua americana (Caesalpiniaceae) at Paracou, French Guiana. — Journal of Tropical Ecology 15: 301-313.

Getzin, S. et al. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. — Ecography 29: 671-682.

Getzin, S. et al. 2010. Size dominance regulates tree spacing more than competition within height classes in tropical Cameroon. — Journal of Tropical Ecology 27: 93-102.

Gibson, N. and Brown, M. J. 1991. The ecology of Lagarostrobos-Franklinii (Hook F) Quinn (Podocarpaceae) in Tasmania: Population-structure and spatial pattern. — Australian Journal of Ecology 16: 223-229.

Gray, L. and He, F. L. 2009. Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. — Forest Ecology and Management 259: 98-106.

Guo, Y. et al. 2013. Spatial distribution of tree species in a species-rich subtropical mountain forest in central China. — Canadian Journal of Forest Research 43: 826-835.

Hai, N. H. et al. 2014. Spatial distributions of tropical tree species in northern Vietnam under environmentally variable site conditions. — Journal of Forestry Research 25: 257-268.

Hao, Z. et al. 2007. Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. — Forest Ecology and Management 252: 1-11.

Hatton, T. J. 1989. Spatial-Analysis of a sub-alpine heath woodland. — Australian Journal of Ecology 14: 65-75.

Hou, J. H. et al. 2004. Spatial patterns and associations in a Quercus-Betula forest in northern China. — Journal of Vegetation Science 15: 407-414.

Hurst, J. M. et al. 2012. Determinants of tree mortality in mixed old-growth Nothofagus forest. — Forest Ecology and Management 270: 189-199.

Isabel Vallejo, M. and Galeano, G. 2009. Short-term temporal changes in the spatial patterns of nine species of common plants in an Andean cloud forest in southwestern Colombia. — Caldasia 31: 77-98.

Janik, D. et al. 2013. Spatiotemporal differences in tree spatial patterns between alluvial hardwood and mountain fir-beech forests: do characteristic patterns exist? — Journal of Vegetation Science 24: 1141-1153.

Kenkel, N. C. 1988. Patten of self-thinning in Jack Pine: testing the random mortality hypothesis. — Ecology 69: 1017-1024.

Kubota, Y. et al. 2007. Spatial pattern dynamics over 10 years in a conifer/broadleaved forest, northern Japan. — Plant Ecology 190: 143-157.

Lamedica, S. et al. 2011. Spatial structure in four Norway spruce stands with different management history in the Alps and Carpathians. — Silva Fennica 5: 895-973.

Lan, G. et al. 2012. Spatial Distribution and Interspecific Associations of Tree Species in a Tropical Seasonal Rain Forest of China. — PLoS ONE 7:

Lawes, M. J. et al. 2008. Tree spacing and area of competitive influence do not scale with tree size in an African rain forest. — Journal of Vegetation Science 19: 729-738.

Lawton, R. M. and Lawton, R. O. 2010. Complex spatial structure in a population of Didymopanax pittieri, a tree of wind-exposed lower montane rain forest. — Plant Ecology 210: 125-135.

Lin, Y. C. et al. 2011. Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. — Oecologia 165: 175-184.

Liu, Y. et al. 2014. Spatial patterns and associations of four species in an old-growth temperate forest. — Journal of Plant Interactions 9: 745-753.

Longuetaud, F. et al. 2008. Analysis of long-term dynamics of crowns of sessile oaks at the stand level by means of spatial statistics. — Forest Ecology and Management 255: 2007-2019.

Luo, Z. R. et al. 2012. Spatial associations of tree species in a subtropical evergreen broad-leaved forest. — Journal of Plant Ecology 5: 346-355.

Lutz, J. A. et al. 2012. Ecological Importance of Large-Diameter Trees in a Temperate Mixed-Conifer Forest. — PLoS ONE 7: e36131.

Maltez-Mouro, S. et al. 2007. Recruitment patterns in a Mediterranean oak forest: A case study showing the importance of the spatial component. — Forest Science 53: 645-652.

Manabe, T. et al. 2000. Population structure and spatial patterns for trees in a temperate old-growth evergreen broad-leaved forest in Japan. — Plant Ecology 151: 181-197.

Martens, S. N. et al. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. — Ecological Modelling 126: 79-93.

Martinez, I. et al. 2010. Spatial associations among tree species in a temperate forest community in North-western Spain. — Forest Ecology and Management 260: 456-465.

Mast, J. N. and Wolf, J. J. 2004. Ecotonal changes and altered tree spatial patterns in lower mixed-conifer forests, Grand Canyon National Park, Arizona, USA. — Landscape Ecology 19: 167-180.

Mast, J. N. and Wolf, J. J. 2006. Spatial patch patterns and altered forest structure in middle elevation versus upper ecotonal mixed-conifer forests, Grand Canyon National Park, Arizona, USA. — Forest Ecology and Management 236: 241-250.

Metsaranta, J. M. and Lieffers, V. J. 2008. A fifty-year reconstruction of annual changes in the spatial distribution of Pinus banksiana stands: does pattern fit competition theory? — Plant Ecology 199: 137-152.

Moeur, M. 1997. Spatial models of competition and gap dynamics in old-growth Tsuga heterophylla Thuja plicata forests. — Forest Ecology and Management 94: 175-186.

Moustakas, A. et al. 2008. Spacing patterns of an Acacia tree in the Kalahari over a 61-year period: How clumped becomes regular and vice versa. — Acta Oecologica 33: 355-364.

Murphy, S. J. and McCarthy, B. C. 2012. Evidence for topographic control of tree spatial patterning in an old-growth, mixed mesophytic forest in Southeastern Ohio, USA. — Journal of the Torrey Botanical Society 139: 181-193.

Nanami, S. et al. 2011. Spatial pattern formation and relative importance of intra- and interspecific competition in codominant tree species, Podocarpus nagi and Neolitsea aciculata. — Ecological Research 26: 37-46.

Navarro-Cerrillo, R. M. et al. 2013. Structure and spatio-temporal dynamics of cedar forests along a management gradient in the Middle Atlas, Morocco. — Forest Ecology and Management 289: 341-353.

Nguyen, H. et al. 2014. Spatial patterns and demographics of Streblus macrophyllus trees in a tropical evergreen forest, Vietnam. — Journal of Tropical Forest Science 26: 309-319.

North, M. et al. 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. — Forest Science 50: 299-311.

Park, A. 2003. Spatial segregation of pines and oaks under different fire regimes in the Sierra Madre Occidental. — Plant Ecology 169: 1-20.

Pellissier, L. et al. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. — Ecography 33: 1004-1014.

Peterson, C. J. and Squiers, E. R. 1995. An Unexpected Change in Spatial Pattern Across 10 Years in an Aspen-White Pine Forest. — Journal of Ecology 83: 847-855.

Petritan, I. C. et al. 2014. Overstory succession in a mixed Quercus petraea-Fagus sylvatica old growth forest revealed through the spatial pattern of competition and mortality. — Forest Ecology and Management 326: 9-17.

Rozas, V. 2003. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech–oak lowland forest in Northern Spain. — Forest Ecology and Management 182: 175-194.

Rozas, V. 2006. Structural heterogeneity and tree spatial patterns in an old-growth deciduous lowland forest in Cantabria, northern Spain. — Plant Ecology 185: 57-72.

Salas, C. et al. 2006. Spatial patterns in an old-growth Nothofagus obliqua forest in south-central Chile. — Forest Ecology and Management 231: 38-46.

Sebkova, B. et al. 2011. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. — Forest Ecology and Management 262: 873-885.

Soto, D. P. et al. 2010. Structural and spatial heterogeneity of a mixed Nothofagus dombeyi-dominated forest stand after a partial disturbance. — Revista Chilena De Historia Natural 83: 335-347.

Tonon, G. et al. 2005. Spatial dynamics of late successional species under Pinus nigra stands in the northern Apennines (Italy). — Annals of Forest Science 62: 669-679.

Vacchiano, G. et al. 2011. Point pattern analysis of crown-to-crown interactions in mountain forests. — Procedia Environmental Sciences 7: 269-274.

Wang, Y. et al. 2010. Analysis of spatial pattern and competition relationship of shrub community in arid desert of Western Ordos Plateau. — Journal of Plant Resources and Environment 19: 8-14.

Ward, J. S. et al. 1996. Long-term spatial dynamics in an old-growth deciduous forest. — Forest Ecology and Management 83: 189-202.

Wells, M. L. and Getis, A. 1999. The spatial characteristics of stand structure in *Pinus torreyana*. — Plant Ecology 143: 153-170.

West, P. W. 1984. Inter-tree competition and small-scale pattern in monoculture of *Eucalpytus obiqua* L'Herit. — Australian Journal of Ecology 9: 405-411.

Wiegand, T. et al. 2007. Species associations in a heterogeneous Sri Lankan dipterocarp forest. — Am Nat 170: E77-95.

Wild, J. et al. 2014. Spatial patterns with memory: tree regeneration after stand-replacing disturbance in *Picea abies* mountain forests. — Journal of Vegetation Science 25: 1327-1340.

Wolf, A. 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. — Forest Ecology and Management 215: 212-223.

Yu, H. et al. 2009. The impact of fire and density-dependent mortality on the spatial patterns of a pine forest in the Hulun Buir sandland, Inner Mongolia, China. — Forest Ecology and Management 257: 2098-2107.

Zagidullina, A. and Tikhodeyeva, M. 2006. Spatial patterns of tree regeneration and ground cover in dry Scots pine forest in Russian Karelia. — Ecoscience 13: 203-218.

Zhang, Q. et al. 2012. Dynamic analysis on spatial pattern of dominant tree species of cold-temperate coniferous forest in the succession process in the Pangquangou Nature Reserve. — Shengtai Xuebao/ Acta Ecologica Sinica 32: 5713-5720.

Zhang, Z.-H. et al. 2010. Spatial patterns and interspecific associations of dominant tree species in two old-growth karst forests, SW China. — Ecological Research 25: 1151-1160.

Zhang, Z. et al. 2013. Aggregated spatial distributions of species in a subtropical karst forest, southwestern China. — Journal of Plant Ecology 6: 131-140.

Zhu, Y. et al. 2013. The Relative Importance of Janzen-Connell Effects in Influencing the Spatial Patterns at the Gutianshan Subtropical Forest. — Plos One 8:

Zhu, Y. et al. 2010. Density dependence is prevalent in a heterogeneous subtropical forest. — Oikos 119: 109-119.

Appendix 2

Chapter IV: LATITUDINAL CONTROLS ON FOREST SPECIES RICHNESS ARE NOT DIRECT

Supplementary Material - Path-analysis detailed results

Library used: lavaan

Function: komatsu

```
summary(lavaan(model=forest,data=z,auto.var=TRUE,fixed.x=FALSE
),rsquare=T)

lavaan (0.5-23.1097) converged normally after 210 iterations


  Number of observations                           195


  Estimator                                         ML
  Minimum Function Test Statistic              805.867
  Degrees of freedom                                36
  P-value (Chi-square)                           0.000


Parameter Estimates:


  Information                                 Expected
  Standard Errors                             Standard


Regressions:
                   Estimate  Std.Err  z-value  P(|z|)
  density ~
    afro             -0.175    0.178   -0.986    0.324
    aust             -0.954    0.200   -4.778    0.000
    indo              0.175    0.183    0.955    0.340
    nearct           -0.010    0.204   -0.050    0.960
```

neotr	-0.204	0.177	-1.149	0.250
temp	-0.103	0.158	-0.654	0.513
dry	0.014	0.152	0.089	0.929
moist	0.227	0.157	1.446	0.148
lat	-0.261	0.092	-2.840	0.005
lat2	0.054	0.166	0.324	0.746
mat	-0.273	0.143	-1.908	0.056
map	-0.279	0.060	-4.627	0.000
evap	0.319	0.121	2.630	0.009
rich ~				
afro	-0.288	0.160	-1.800	0.072
aust	-1.091	0.180	-6.074	0.000
indo	-0.167	0.164	-1.015	0.310
nearct	-0.174	0.184	-0.946	0.344
neotr	-0.044	0.159	-0.275	0.783
temp	0.822	0.142	5.779	0.000
dry	0.815	0.136	5.975	0.000
moist	1.001	0.141	7.103	0.000
lat	-0.115	0.083	-1.397	0.163
lat2	-0.281	0.150	-1.881	0.060
mat	0.067	0.129	0.524	0.600
map	-0.055	0.054	-1.008	0.314
evap	0.292	0.109	2.677	0.007
evar ~				
afro	-0.083	0.035	-2.360	0.018
aust	-0.081	0.039	-2.052	0.040
indo	-0.124	0.036	-3.440	0.001

nearct	-0.073	0.040	-1.806	0.071
neotr	-0.077	0.035	-2.214	0.027
temp	0.101	0.031	3.246	0.001
dry	0.129	0.030	4.319	0.000
moist	0.120	0.031	3.878	0.000
lat	0.014	0.018	0.751	0.453
lat2	-0.014	0.033	-0.426	0.670
mat	0.096	0.028	3.423	0.001
map	0.071	0.012	6.006	0.000
evap	-0.100	0.024	-4.196	0.000
area ~				
afro	0.520	0.264	1.969	0.049
aust	0.639	0.296	2.155	0.031
indo	0.539	0.272	1.985	0.047
nearct	0.212	0.303	0.700	0.484
neotr	0.592	0.263	2.249	0.025
temp	0.435	0.235	1.854	0.064
dry	0.406	0.225	1.805	0.071
moist	0.699	0.233	3.003	0.003
lat	0.144	0.137	1.057	0.291
lat2	0.201	0.247	0.814	0.415
mat	0.061	0.212	0.289	0.773
map	-0.138	0.090	-1.541	0.123
evap	0.171	0.180	0.948	0.343
temp ~				
lat	-0.079	0.021	-3.824	0.000
lat2	0.307	0.063	4.890	0.000

mat	-0.123	0.054	-2.284	0.022
map	-0.151	0.024	-6.316	0.000
evap	0.117	0.038	3.041	0.002
dry ~				
lat	-0.012	0.022	-0.577	0.564
lat2	-0.028	0.066	-0.433	0.665
mat	0.412	0.056	7.331	0.000
map	0.097	0.025	3.866	0.000
evap	-0.443	0.040	-11.057	0.000
moist ~				
lat	0.043	0.021	2.077	0.038
lat2	-0.304	0.063	-4.796	0.000
mat	-0.284	0.054	-5.213	0.000
map	0.050	0.024	2.075	0.038
evap	0.328	0.039	8.468	0.000
mat ~				
lat	-0.027	0.027	-1.021	0.307
lat2	-0.916	0.027	-34.473	0.000
map ~				
lat	-0.093	0.060	-1.545	0.122
lat2	-0.461	0.060	-7.703	0.000
evap ~				
lat	-0.105	0.037	-2.798	0.005
lat2	-0.815	0.037	-21.859	0.000

Covariances:

	Estimate	Std.Err	z-value	P(|z|)

.density ~~				
.area	-0.156	0.042	-3.689	0.000
.rich ~~				
.area	0.118	0.038	3.122	0.002
.evar ~~				
.area	-0.051	0.009	-5.787	0.000
.density ~~				
.rich	0.031	0.025	1.249	0.212
.rich ~~				
.evar	0.014	0.005	2.778	0.005
.density ~~				
.evar	-0.018	0.006	-3.290	0.001
afro ~~				
aust	-0.040	0.012	-3.383	0.001
indo	-0.024	0.010	-2.543	0.011
nearct	-0.026	0.010	-2.641	0.008
neotr	-0.022	0.009	-2.391	0.017
lat	0.010	0.027	0.373	0.709
lat2	-0.166	0.029	-5.671	0.000
aust ~~				
indo	-0.036	0.011	-3.202	0.001
nearct	-0.038	0.012	-3.323	0.001
neotr	-0.032	0.011	-3.014	0.003
lat	-0.297	0.037	-7.949	0.000
lat2	0.189	0.034	5.623	0.000
indo ~~				
nearct	-0.024	0.009	-2.497	0.013

neotr	-0.020	0.009	-2.259	0.024
lat	0.092	0.026	3.470	0.001
lat2	-0.088	0.026	-3.338	0.001
nearct ~~				
neotr	-0.021	0.009	-2.347	0.019
lat	0.223	0.031	7.244	0.000
lat2	0.168	0.029	5.793	0.000
neotr ~~				
lat	-0.023	0.024	-0.924	0.355
lat2	-0.109	0.026	-4.233	0.000
lat ~~				
lat2	0.054	0.072	0.748	0.455

Variances:

	Estimate	Std.Err	z-value	P(|z|)
.temp	0.079	0.008	9.874	0.000
.dry	0.086	0.009	9.874	0.000
.moist	0.080	0.008	9.874	0.000
.mat	0.139	0.014	9.874	0.000
.map	0.705	0.071	9.874	0.000
.evap	0.274	0.028	9.874	0.000
.area	0.848	0.086	9.874	0.000
.density	0.384	0.039	9.874	0.000
.evar	0.015	0.002	9.874	0.000
.rich	0.311	0.031	9.874	0.000
afro	0.137	0.014	9.874	0.000
aust	0.183	0.019	9.874	0.000

indo	0.127	0.013	9.874	0.000
nearct	0.134	0.014	9.874	0.000
neotr	0.116	0.012	9.874	0.000
lat	1.008	0.102	9.874	0.000
lat2	1.012	0.103	9.874	0.000

R-Square:

	Estimate
temp	0.698
dry	0.518
moist	0.660
mat	0.860
map	0.245
evap	0.717
area	0.147
density	0.302
evar	0.528
rich	0.759

```
 # STRIPPED-DOWN ANALYSES (lat2 is more important without the
extra layers)


 forest = '
+    rich ~ temp + dry + moist + lat2
+    rich ~~ rich
+ '
```

```
 forest = '
+    rich ~ temp + dry + moist + lat2
+    rich ~~ rich
+    temp ~ lat2
+    dry ~ lat2
+    moist ~ lat2
+    temp ~~ temp
+    dry ~~ dry
+    moist ~~ moist
+ '



 # NEOTROPICS ONLY
 # temp has to be dropped out



 z2 = z[which(z[,'neotr'] == 1),]
 z2 = z2[,6:ncol(z2)]


 forest = '
+    density + rich + evar + area ~ dry + moist + lat + lat2 +
mat + map + evap
+    dry ~ lat + lat2 + mat + map + evap
+    moist ~ lat + lat2 + mat + map + evap
+    mat ~ lat + lat2
+    map ~ lat + lat2
+    evap ~ lat + lat2
+    area ~~ density
```

```
+    area ~~ rich
+    area ~~ evar
+    density ~~ rich
+    evar ~~ rich
+    density ~~ evar
+    dry ~~ dry
+    moist ~~ moist
+    mat ~~ mat
+    map ~~ map
+    evap ~~ evap
+    area ~~ area
+    density ~~ density
+    evar ~~ evar
+    rich ~~ rich
+ '
```

```
summary(lavaan(model=forest,data=z2,auto.var=TRUE,fixed.x=FALS
E),rsquare=T)
```

```
lavaan (0.5-23.1097) converged normally after 127 iterations
```

```
  Number of observations                            26

  Estimator                                         ML
  Minimum Function Test Statistic               90.650
  Degrees of freedom                                 4
  P-value (Chi-square)                           0.000
```

Parameter Estimates:

Information				Expected
Standard Errors				Standard

Regressions:

	Estimate	Std.Err	z-value	P(|z|)
density ~				
dry	1.423	0.219	6.482	0.000
moist	1.658	0.237	6.998	0.000
lat	-0.416	0.155	-2.679	0.007
lat2	1.017	0.402	2.531	0.011
mat	-0.462	0.308	-1.499	0.134
map	-0.532	0.097	-5.473	0.000
evap	0.700	0.285	2.453	0.014
rich ~				
dry	0.097	0.442	0.219	0.827
moist	0.913	0.478	1.911	0.056
lat	-0.449	0.313	-1.432	0.152
lat2	-0.302	0.809	-0.373	0.709
mat	0.925	0.621	1.489	0.137
map	0.113	0.196	0.577	0.564
evap	-0.360	0.575	-0.626	0.531
evar ~				
dry	0.174	0.052	3.313	0.001
moist	0.281	0.057	4.967	0.000
lat	-0.026	0.037	-0.709	0.478

lat2	0.180	0.096	1.876	0.061
mat	0.211	0.074	2.867	0.004
map	0.053	0.023	2.276	0.023
evap	-0.081	0.068	-1.182	0.237
area ~				
dry	-3.055	0.342	-8.941	0.000
moist	-3.286	0.369	-8.907	0.000
lat	0.169	0.242	0.696	0.486
lat2	-2.558	0.625	-4.092	0.000
mat	-0.217	0.480	-0.453	0.650
map	0.102	0.151	0.674	0.500
evap	-0.332	0.444	-0.748	0.455
dry ~				
lat	0.118	0.137	0.863	0.388
lat2	-0.283	0.338	-0.837	0.403
mat	0.661	0.190	3.487	0.000
map	0.189	0.072	2.621	0.009
evap	-0.817	0.128	-6.364	0.000
moist ~				
lat	0.012	0.127	0.093	0.926
lat2	-0.499	0.313	-1.591	0.112
mat	-0.717	0.176	-4.080	0.000
map	-0.150	0.067	-2.253	0.024
evap	0.712	0.119	5.985	0.000
mat ~				
lat	0.168	0.129	1.304	0.192
lat2	-0.896	0.202	-4.433	0.000

map ~				
lat	0.484	0.340	1.423	0.155
lat2	-1.172	0.533	-2.200	0.028
evap ~				
lat	0.238	0.191	1.250	0.211
lat2	-1.563	0.298	-5.238	0.000

Covariances:

	Estimate	Std.Err	z-value	P(|z|)
.density ~~				
.area	-0.005	0.030	-0.166	0.868
.rich ~~				
.area	0.152	0.067	2.263	0.024
.evar ~~				
.area	-0.007	0.007	-0.943	0.346
.density ~~				
.rich	0.055	0.040	1.375	0.169
.rich ~~				
.evar	0.031	0.011	2.799	0.005
.density ~~				
.evar	-0.001	0.005	-0.176	0.860
lat ~~				
lat2	-0.056	0.030	-1.844	0.065

Variances:

	Estimate	Std.Err	z-value	P(|z|)
.dry	0.078	0.022	3.606	0.000

.moist	0.067	0.019	3.606	0.000
.mat	0.083	0.023	3.606	0.000
.map	0.578	0.160	3.606	0.000
.evap	0.182	0.050	3.606	0.000
.area	0.236	0.066	3.606	0.000
.density	0.098	0.027	3.606	0.000
.evar	0.006	0.002	3.606	0.000
.rich	0.396	0.110	3.606	0.000
lat	0.226	0.063	3.606	0.000
lat2	0.092	0.026	3.606	0.000

R-Square:

	Estimate
dry	0.701
moist	0.754
mat	0.539
map	0.296
evap	0.607
area	0.862
density	0.872
evar	0.694
rich	0.366

```
 # BASAL AREA INCLUDED


 z                                                                  =
cbind(afro,aust,indo,nearct,neotr,temp,dry,moist,t2[,c('lat','
mat','map','evap','ba','area','rich','evar')],density)

 z[,'lat2'] = z[,'lat']^2

 z[,'map'] = sqrt(z[,'map'])

 z[,'evap'] = sqrt(z[,'evap'])

 z[,'ba'] = log(z[,'ba'])

 z[,'area'] = log(z[,'area'])

 z[,'density'] = log(z[,'density'])

 z[,'rich'] = log(z[,'rich'])


 z[,'lat'] = scale(z[,'lat'])

 z[,'lat2'] = scale(z[,'lat2'])

 z[,'mat'] = scale(z[,'mat'])

 z[,'map'] = scale(z[,'map'])

 z[,'evap'] = scale(z[,'evap'])

 z[,'area'] = scale(z[,'area'])


 forest = '

+    ba + density + rich + evar + area ~ afro + aust + indo +
nearct + neotr + temp + dry + moist + lat + lat2 + mat + map +
evap

+    temp ~ lat + lat2 + mat + map + evap

+    dry ~ lat + lat2 + mat + map + evap

+    moist ~ lat + lat2 + mat + map + evap

+    mat ~ lat + lat2

+    map ~ lat + lat2
```

```
+    evap ~ lat + lat2
+    ba ~~ area
+    ba ~~ density
+    ba ~~ rich
+    ba ~~ evar
+    area ~~ density
+    area ~~ rich
+    area ~~ evar
+    density ~~ rich
+    evar ~~ rich
+    density ~~ evar
+    temp ~~ temp
+    dry ~~ dry
+    moist ~~ moist
+    mat ~~ mat
+    map ~~ map
+    evap ~~ evap
+    ba ~~ ba
+    area ~~ area
+    density ~~ density
+    evar ~~ evar
+    rich ~~ rich
+ '



summary(lavaan(model=forest,data=z,auto.var=TRUE,fixed.x=FALSE
),rsquare=T)

lavaan (0.5-23.1097) converged normally after 234 iterations
```

	Used	Total
Number of observations	154	215

Estimator	ML
Minimum Function Test Statistic	702.330
Degrees of freedom	36
P-value (Chi-square)	0.000

Parameter Estimates:

Information	Expected
Standard Errors	Standard

Regressions:

	Estimate	Std.Err	z-value	P(|z|)
ba ~				
afro	-0.114	0.161	-0.709	0.478
aust	-0.097	0.203	-0.478	0.633
indo	0.203	0.169	1.205	0.228
nearct	0.031	0.200	0.156	0.876
neotr	-0.338	0.160	-2.119	0.034
temp	0.004	0.141	0.027	0.979
dry	-0.346	0.132	-2.614	0.009
moist	-0.281	0.137	-2.058	0.040
lat	-0.288	0.099	-2.905	0.004
lat2	-0.002	0.160	-0.013	0.990

mat	0.271	0.130	2.093	0.036
map	0.478	0.054	8.860	0.000
evap	-0.648	0.107	-6.057	0.000
density ~				
afro	-0.083	0.183	-0.453	0.651
aust	-0.999	0.230	-4.339	0.000
indo	0.431	0.191	2.254	0.024
nearct	-0.019	0.227	-0.084	0.933
neotr	-0.227	0.181	-1.254	0.210
temp	-0.094	0.159	-0.591	0.555
dry	-0.000	0.150	-0.003	0.998
moist	0.222	0.155	1.430	0.153
lat	-0.280	0.112	-2.490	0.013
lat2	0.101	0.182	0.554	0.580
mat	-0.078	0.147	-0.534	0.594
map	0.012	0.061	0.199	0.842
evap	-0.054	0.121	-0.442	0.658
rich ~				
afro	-0.215	0.171	-1.261	0.207
aust	-1.414	0.215	-6.582	0.000
indo	0.073	0.178	0.411	0.681
nearct	-0.080	0.212	-0.376	0.707
neotr	0.073	0.169	0.430	0.667
temp	0.854	0.149	5.746	0.000
dry	0.937	0.140	6.697	0.000
moist	1.089	0.144	7.541	0.000
lat	-0.299	0.105	-2.852	0.004

lat2	-0.272	0.170	-1.605	0.109
mat	0.019	0.137	0.136	0.892
map	-0.076	0.057	-1.326	0.185
evap	0.271	0.113	2.394	0.017
evar ~				
afro	-0.088	0.038	-2.283	0.022
aust	-0.051	0.048	-1.055	0.291
indo	-0.138	0.040	-3.428	0.001
nearct	-0.099	0.048	-2.080	0.038
neotr	-0.055	0.038	-1.454	0.146
temp	0.111	0.033	3.302	0.001
dry	0.127	0.032	4.021	0.000
moist	0.115	0.033	3.520	0.000
lat	0.040	0.024	1.679	0.093
lat2	-0.026	0.038	-0.689	0.491
mat	0.069	0.031	2.236	0.025
map	0.030	0.013	2.327	0.020
evap	-0.046	0.025	-1.789	0.074
area ~				
afro	0.537	0.277	1.934	0.053
aust	0.545	0.349	1.559	0.119
indo	0.438	0.290	1.509	0.131
nearct	0.203	0.344	0.591	0.555
neotr	0.498	0.275	1.812	0.070
temp	0.364	0.242	1.506	0.132
dry	0.575	0.228	2.528	0.011
moist	0.858	0.235	3.649	0.000

lat	0.029	0.170	0.171	0.864
lat2	0.238	0.276	0.861	0.389
mat	0.006	0.223	0.025	0.980
map	-0.154	0.093	-1.653	0.098
evap	0.210	0.184	1.140	0.254
temp ~				
lat	-0.099	0.023	-4.219	0.000
lat2	0.358	0.077	4.671	0.000
mat	0.042	0.065	0.644	0.520
map	-0.047	0.030	-1.573	0.116
evap	-0.070	0.044	-1.571	0.116
dry ~				
lat	-0.009	0.025	-0.351	0.725
lat2	-0.091	0.081	-1.120	0.263
mat	0.354	0.069	5.104	0.000
map	0.080	0.032	2.529	0.011
evap	-0.422	0.047	-8.938	0.000
moist ~				
lat	0.051	0.024	2.102	0.036
lat2	-0.267	0.079	-3.388	0.001
mat	-0.295	0.067	-4.391	0.000
map	0.061	0.031	2.005	0.045
evap	0.348	0.046	7.612	0.000
mat ~				
lat	-0.013	0.028	-0.486	0.627
lat2	-0.940	0.029	-32.894	0.000
map ~				

lat	-0.127	0.061	-2.093	0.036
lat2	-0.510	0.063	-8.147	0.000
evap ~				
lat	-0.122	0.041	-2.998	0.003
lat2	-0.832	0.042	-19.833	0.000

Covariances:

	Estimate	Std.Err	z-value	P(|z|)
.ba ~~				
.area	0.012	0.034	0.352	0.725
.density	0.060	0.023	2.602	0.009
.rich	0.038	0.021	1.817	0.069
.evar	-0.005	0.005	-1.073	0.283
.density ~~				
.area	-0.107	0.040	-2.702	0.007
.rich ~~				
.area	0.077	0.037	2.102	0.036
.evar ~~				
.area	-0.043	0.009	-4.911	0.000
.density ~~				
.rich	0.031	0.024	1.308	0.191
.rich ~~				
.evar	0.014	0.005	2.698	0.007
.density ~~				
.evar	-0.019	0.006	-3.460	0.001
afro ~~				
aust	-0.040	0.013	-3.078	0.002

indo	-0.018	0.009	-1.883	0.060
nearct	-0.020	0.010	-2.032	0.042
neotr	-0.015	0.009	-1.727	0.084
lat	0.016	0.028	0.587	0.557
lat2	-0.137	0.029	-4.729	0.000
aust ~~				
indo	-0.042	0.013	-3.160	0.002
nearct	-0.048	0.014	-3.399	0.001
neotr	-0.036	0.012	-2.909	0.004
lat	-0.348	0.047	-7.392	0.000
lat2	0.222	0.041	5.433	0.000
indo ~~				
nearct	-0.021	0.010	-2.089	0.037
neotr	-0.016	0.009	-1.775	0.076
lat	0.099	0.029	3.375	0.001
lat2	-0.091	0.028	-3.225	0.001
nearct ~~				
neotr	-0.018	0.010	-1.917	0.055
lat	0.240	0.036	6.749	0.000
lat2	0.158	0.032	5.002	0.000
neotr ~~				
lat	-0.013	0.026	-0.509	0.610
lat2	-0.105	0.027	-3.874	0.000
lat ~~				
lat2	0.018	0.081	0.218	0.828

Variances:

	Estimate	Std.Err	z-value	P(|z|)
.temp	0.081	0.009	8.775	0.000
.dry	0.091	0.010	8.775	0.000
.moist	0.085	0.010	8.775	0.000
.mat	0.123	0.014	8.775	0.000
.map	0.593	0.068	8.775	0.000
.evap	0.266	0.030	8.775	0.000
.ba	0.246	0.028	8.775	0.000
.area	0.726	0.083	8.775	0.000
.density	0.316	0.036	8.775	0.000
.evar	0.014	0.002	8.775	0.000
.rich	0.275	0.031	8.775	0.000
afro	0.113	0.013	8.775	0.000
aust	0.212	0.024	8.775	0.000
indo	0.118	0.013	8.775	0.000
nearct	0.132	0.015	8.775	0.000
neotr	0.103	0.012	8.775	0.000
lat	1.041	0.119	8.775	0.000
lat2	0.981	0.112	8.775	0.000

R-Square:

	Estimate
temp	0.674
dry	0.467
moist	0.621
mat	0.876
map	0.317

evap	0.724
ba	0.574
area	0.185
density	0.226
evar	0.484
rich	0.808

Appendix 3

Chapter V: LOOK DOWN TO SEE WHAT'S UP: A SYSTEMATIC OVERVIEW OF TREEFALL DYNAMICS IN FORESTS

Table Appendix 3. Studies of treefall and its legacy effects, categorised according to the four most commonly studied research themes; causes, characteristics of the trees that contribute to treefall, causes of treefall events, and management/modelling applications. The most highly cited studies within each three-year block from 1985 to 2016 were chosen. In cases where the categories were extremely broad, additional studies were included to provide a more representative sampling of the breadth of the literature on that subtopic.

Footnote:

^ Study type: field measurements (FM), field experiment (FE), review (R), modelling (M), glasshouse (GH), experiment in the field (EF), lab experiment (EL), management (MM).

* Impact: population (P), community (C), ecosystem (E), landscape (L), individual (I).

Date	Author(s)	Forest type	Topic of paper	Study type^		Key development or finding	Cites	Terms used
CONSEQUENCES ***Canopy gaps and gap dynamics***								
1985 1986 1987	(Brokaw, 1987)	Tropical forest	Gap-phase regeneration behaviour examined for three tree species in natural gaps during the first 8-9 years of growth.	FM	C	Diversity in growth, recruitment and gap-size requirements across different species, that maintains diversity within gaps; but some overlap in regeneration behaviours may favour coexistence among some species.	385	Gap-phase regeneration, gaps
1988 1989 1990	(Denslow *et al.*, 1990)	Tropical rainforest	Exploring the potential differences in light and nutrient availability on growth, in treefall gaps.	E/GH	C	The amount of light available in treefall gaps is important for the persistence, and co-existence of species (esp. shade-intolerant sp.)	335	Treefall gap, gaps

1988 1989 1990	(Canham *et al.*, 1990)	Temperate and tropical forests	Assessment of light intensity /regimes beneath closed canopies and tree-fall gaps.	FM	C	Under intact canopies sun flecks contribute 37-68% of seasonal radiation and light is generally not vertical. Light can penetrate into gap-edges. As gap size increases the mean and range of light within gap increases, but even in large gaps the potential duration of direct sunlight is restricted to approx. <4h.	823	Tree-fall gaps, forest canopies, gaps, gap light regimes
1988 1989 1990	(Whitmore, 1989)	All forest types	Review of the role of gap size and succession within gaps for recruitment.	R	P	Our present knowledge of forest dynamics is highlighted by the existence of forest cycles, gaps and the division of tree species into two groups: climax and pioneer species (which is related to their persistence in varying light environments).	924	Canopy gaps, gap, gap size
1991 1992 1993	(Rebertus & Veblen, 1993)	*Nothofagus* forest	Characterising the dynamics and regeneration strategies of the broad latitudinal-ranged *Nothofagus* species	FM	P	Regeneration in gaps appears to be adequate to maintain the structure and composition of the old-growth forests studied.	188	Tree-fall gap, tree-fall, gap-phase, regeneration

1994 1995 1996	(Kuuluvainen, 1994)	Boreal forest	A review of gap disturbance, ground micro topography and regeneration dynamics in boreal forests.	R	E	Understanding of the ecological significance of small-scale gap disturbances in boreal forests is limited. Patch mosaic structure has been altered by forest management.	293	Gap disturbance, gap, treefall gap
1997 1998 1999	(Denslow *et al.*, 1998)	Tropical (wet) forest	Effect of variation in gap size on above- and below-ground light and nutrient processes.	EF&EL	C	Higher nutrient pools in gaps caused by decomposition and mineralisation of the woody debris. This increase effects the high-or light-demanding species much more than shade-tolerant.	285	Treefall gap, gaps, treefalls
2000 2001 2002	(Schnitzer & Carson, 2001)	Tropical forest	Critique of the paradigm: 'Treefall gaps maintain species diversity'.	FM	C	Gaps did not appear to increase diversity of shade-tolerant tree species, but it did for liana and pioneer tree species diversity.	362	Treefall gaps, gaps
2003 2004 2005	(Ritter *et al.*, 2005)	Beech forest	Effect of gap formation (over time) on the physical environment (light, temperature and soil moisture)	EF&FM	C	Growth of regeneration of 'edge trees' (as a result of increased light, shading and water extraction by roots) may have modified the	152	Gap dynamics, gap, canopy opening

						effects of the canopy gap as early as the second year of gap formation.		
2006 2007 2008	(Galhidy *et al.*, 2006)	Beech forest	Effect of gap size on light and soil moisture in the gap on abundance and distribution of herb layer species.	FE	C	Gap size had a profound effect on environmental variables but its effects were species-specific.	107	Gap, canopy gaps, gap size, gap formation
2009 2010 2011	(Gravel *et al.*, 2010)	All forest types	How does low light survival and high light growth allow coexistence - and what are the limitations.	R	P	Present/propose a theory of forest dynamics driven by small-scale disturbances as a species case of coexistence in variable environments. While low light survival/high light growth trade-off, while ubiquitous in forests, is unlikely to function as an important mechanism for stable coexistence of several tree species.	44	Gaps, canopy gaps, coexistence, canopy disturbance

2012 2013 2014	(Forrester *et al.*, 2012)	Hardwood forest	How the environmental conditions in gaps influence the decomposition and accumulation of coarse-woody debris.	FE	C	CWD in canopy gaps experience greater surface temperatures and decreased moisture conditions throughout most of the growing season. Annual C fluxes were higher in gaps	38	Coarse woody debris (CWD), canopy gaps, woody debris, gaps
2015 2016	(Hunter *et al.*, 2015)	Tropical forest	Propose a new definition of a forest gap based on precise measurements from airborne LIDAR.	FM	P	Dynamic gaps are "contiguous areas of significant growth, that correspond to areas >10cm2 with height <10m."	0	Gap-phase, gaps, gap dynamics
CAUSES **Small & Large scale** ***Disturbance (Extreme weather events [fire & wind], uprooting)***								
1988 1989 1990	(Schaetzl *et al.*, 1989)	All forest types	Review of tree uprooting (terminology) and its causes and consequences.	R	C	The term uprooting is distinct from treefall tree throw and blowdowns. This is because uprooting explicitly involves soil disturbance, and not 'bole snap'.	113	Uprooting, tree throw, treefall, blowdown, disturbance

1988 1989 1990	(Peterson *et al.*, 1990)	Hardwood forest	Assessed 3 hypotheses: 1) Does micro-site variation exist in pits and mounds; 2) do pit size and soil accumulation matter and 3) do the species that created the pit and mound matter?	FM	C	Pit and mound sizes were proportional to the size of the fallen tree but the identity of the tree did not matter (except in the intact soil microsite), large pits revegetated more slowly than small ones, 4 micro-sites were found in the pit.	173	Treefall pits and mounds & windthrow
1991 1992 1993	(Peterson & Pickett, 1991)	Hardwood forest	Frequency of uprooting versus bole snapping and the influence of these alternative treefalls on sprouting.	FM	C to P	Tree size was the most important factor in determining frequency of uproots vs. snapped trees. Uprooting occurs at a higher frequency in old-growth hardwood forests. Sprouting was determined to be of little importance for re-establishment, especially following a large windthrow event.	129	Uprooting & fallen tree
1991 1992 1993	(Jonsson & Dynesius, 1993)	Boreal spruce forest	Uprooted tree disturbance effect on the forest floor over a long time period (120 years)	FM	C	Uproot tree direction and frequency was strongly correlated to wind disturbance. There were large variations in disturbance rate, with higher rates in some years	65	Uprooting & uprooted trees

						compared to others - this implies periods with low availability of exposed soil.		
1994 1995 1996	(Everham & Brokaw, 1996)	All forest types	A review of the damage and recovery of forests from catastrophic wind disturbance.	R	C to P	Measurement methods between studies can alter the results, leading to different conclusions regarding the severity of disturbance. Wind disturbance creates gaps of differing size, and recovery tends have been summarised here, to follow one of four pathways: regrowth, recruitment, release or repression.	445	Wind damage/disturbance, Treefalls
1997 1998 1999	(Ennos, 1997)	All forest types	A review of the reasons why wind disturbance may be better considered as an ecological factor.	R	P	Studying the mechanical effects of wind (acclimation/adaptation of trees) may be a more important direction to take, as its effects may be greater than the acute effects of destructive storms.	159	Windthrow, treefall, wind

2000 2001 2002	(Kramer *et al.*, 2001)	Coastal temperate rainforest	Investigation of the abiotic factors controlling patterns of long-term windthrow, and how well they can be predicted using spatial information.	FM/M	I to P	Large-scale stand-replacement disturbance processes are common in areas most prone to windthrow, where small-scale disturbance processes are more common in areas least prone to windthrow.	122	Windthrow, gap-phase disturbances
2003 2004 2005	(Fulé *et al.*, 2004)	Conifer forests	Effects of prescribed fire on tree structure over 6 years - and its implications for forest restoration.	FM	C	The ecological outcomes of a prescribed burn in these forests were not in-line with the restoration goals for this ecosystem type: a reduction in tree density, reduction of woody debris and the death of old-growth trees resulted.	94	Fire, trees, coarse woody debris (CWD), forest floor fuels, burning
2006 2007 2008	(Rich *et al.*, 2007)	Boreal forest	Assessment of tree mortality patterns contrasting: differences across tree sizes, wind intensity and stand age.	FM	P	Larger sized trees and old stands were more susceptible to wind-driven mortality. Likewise, early successional and shade intolerant were also more at-risk.	93	Wind-throw, blowdown, wind disturbance

2006 2007 2008	(Phillips & Marion, 2006)	Ouachita Mountains	Studied the biomechanical effects of stump-rot depression and infilling (contrasts to uprooting).	FM	C	Highlights that two other processes are significant to forest disturbance dynamics that should be considered alongside other uprooting effects: the physical displacement of soil by root and trunk growth and the infilling of depressions created by stump rot.	46	Tree throw, uprooting
2009 2010 2011	(Samonil *et al.*, 2009)	Fir-beech forest	Development of methods to quantify the age of windthrow events using field measurements and modelling.	FM/M	C	Age explained 34% of the variability in the measured windthrow associated variables: thickness of soil (on both mounds and pits), presence of new trees recruiting in windthrow areas, and the dimensions of the effect.	56	Windthrow, uprooted trees
2012 2013 2014	(Mitchell, 2012)	All forest types	Synthesis of the impact of wind-caused disturbance at multiple scales for application in forest management.	R	I to P	Windthrow is more than just a catastrophic phenomenon, with reoccurring effects on ecosystem process and pattern. They also call for a more interdisciplinary view on nature and occurrence of wind damage.	50	Windthrow

2015 2016	(Cannon *et al.*, 2015)	Mixed pine-broadleaf forest	Experimentally examine how tree size, species, fire history and failure mode influence tree stability.	FM	I	Tree stability increased with tree size. Their findings suggest that interspecific differences in reported tree damage may be more due to variation in wind load than to innate interspecific differences in tree stability.	0	Wind disturbance, snapping, uprooting, fire, tree stability
CAUSES ***Tree mortality & standing dead/dead wood (CWD)***								
1985 1986 1987	(Lieberman *et al.*, 1985)	Tropical forest	Determining causes and rates of mortality over a 13-year period.	FM	P	Mortality was independent of size among individuals. Of those that died over the 13 years, most had decomposed entirely, or had fallen - a net loss of 1.7% stems across 13 years.	280	Treefall gap, treefalls, mortality
1988 1989 1990	(Tritton & Siccama, 1990)	Spruce-fir forest	Evaluation of the number of (standing) dead trees in Northern spruce-fir forests.	FM	P	Across the 46 datasets, dead trees were determined to account for 3-43% of total basal area and 5-36% of total density - the wide range reflects the complexity and interactions in forests.	32	Standing dead trees, mortality, dead trees

1991 1992 1993	(Greene *et al.*, 1992)	*Tsuga heterophylla* forest	Factors that influence growth and mortality of trees.	FM	C	Rates of tree mortality are high in this forest - it is frequently exposed to severe wind events (disturbance is considered important in this system).	31	Blowdown, mortality, wind, gap
1994 1995 1996	(Guby & Dobbertin, 1996)	Swiss forests	Quantitative assessment of the volume and decay stage of CWD and standing dead trees across sites in the Alps at different elevations.	FM	C	Differences in the volume of dead wood across sites, but high sampling variability. Most of the dead wood = young decay classes. Management of dead wood is paramount, and to fully understand how to manage it, more qualitative and quantitative assessments of CWD must be done across ecosystems and differing environmental conditions.	85	Coarse woody debris (CWD), standing dead trees, dead wood
1994 1995 1996	(Esseen, 1994)	Old-growth conifer forest	Comparison of the structure of fragmented and non-fragmented forests to understand their ecology.	FM	P	Found an increase in mortality following a wind event, but this mortality differed with fragment size - 30% 1ha fragment, 98% in 1/16ha. Of this mortality, uprooting was the most common, followed by stem breakage).	156	Tree mortality, blowdown, uprooting

1997 1998 1999	(Kirby *et al.*, 1998)	Temperate forests	Quantifying the amount of dead wood in various forests in Britain, Europe and North America.	FM	C	Managed forests contained much less fallen dead wood than unmanaged. In British forests, it is unclear whether increasing the amount of dead wood will increase the diversity of these forests.	184	Fallen dead wood, fallen logs, standing dead trees
2000 2001 2002	(He & Duncan, 2000)	Douglas Fir (Df) & Red cedar (Rc) forest	Investigations of density-dependence and mortality with two different component species.	FM	P	Mortality changed the spatial associations between species. Non-random mortality of Df and Rc such that survivors were more strongly aggregated than expected. Found some evidence of density-related effects on tree survival in this study.	242	Density-dependent, dead trees, mortality
2003 2004 2005	(Christensen *et al.*, 2005)	European Beech forest	Quantitative assessments of dead wood volume (standing vs. fallen dead wood) between two contrasting (disturbance regime) forests.	FM	P	Dead wood is largely driven by disturbance (and thus varies over time). Fallen dead wood contributed more to total dead wood than standing dead wood. Windstorm damage is a large contributing factor to	237	Dead wood, standing dead wood, fallen dead wood

						standing dead wood volume, but this also depends on topographic heterogeneity.		
2006 2007 2008	(Aakala *et al.*, 2007)	Old-growth boreal forest	Exploring the spatial, temporal and frequency of standing tree mortality.	FM/M	C	Mortality of standing dead trees (excluding catastrophic disturbance events) is an important process in forest structural complexity and diversity. Standing dead trees in *Pinus* stands were predominately clustered, large dead = random, small dead = clustered.	51	Standing-tree mortality, living and dead trees
2009 2010 2011	(Angers *et al.*, 2010)	Boreal forest	Assessing snag degradation pathways (survival curves) of the main boreal species in North America	FM	C	Diameter of trees did not influence fall probability. Differential degradation pathways were determined for the four species examined that translate individualistic responses that are related to species autecology.	49	Deadwood, snags, logs

2012 2013 2014	(Holzwarth *et al.*, 2013)	Mixed-deciduous beech forest	Prescribing mortality patterns into different processes (i.e., modes of death) to determine how mortality varies among and between species for testing mechanistic models.	M	P	Survival/mortality varied with life-history stage (time); small trees = died standing or crushed, medium-sized trees = lower mortality, large trees = very high mortality rates mostly due to snapping and uprooting.	29	Standing dead, tree mortality, uprooting
2015 2016	(Larson *et al.*, 2015)	Many forest types	Reconciling the spatial aspects of tree mortality in old-growth forests (successional stage).	FM	C	Spatial aspects of tree mortality change over time, particularly in latter successional stages.	3	Tree mortality, density-dependence
CONSEQUENCES ***Decay & nurse logs (recruitment)***								
1985 1986 1987	(Sollins *et al.*, 1987)	Many forest types	Differences in log attributes (structure, chemistry, microbial activity) across three forests.	FM	P	Western hemlock and red cedar logs decayed faster than Douglas fir (which had logs that had persisted 200 yrs). It took 90 yrs for N, P and Mg to exceed initial amounts. Other elements (Ca, K, Na)	199	Fallen boles, logs

						remained constant throughout the 200 yrs studied.		
1988 1989 1990	(Harmon & Franklin, 1989)	*Picea-Tsuga* forest	Causes of close seedling-log associations (how logs facilitate seedling recruitment).	FM	I to C	Competition with herbs and mosses on the forest floor appears to be responsible for the disproportionate number of tree seedlings found on logs. Recently fallen logs represent sites where competition is low enough to facilitate seedling recruitment.	351	Logs, fallen logs, nurse logs, fallen dead tree
1991 1992 1993	(Harmon & Hua, 1991)	Deciduous & conifer forests	Comparison of the amount of CWD and processes that influence CWD accumulation in two different forest systems.	FM/R	P	Lower input and faster decay rates means that there is less CWD in deciduous forest than conifer (there are three-times the number of logs in conifer forest). During gradual mortality, CWD adds fewer nutrients than fine litter at both sites because nutrients are released at slower rates from CWD than litter.	234	Coarse woody debris (CWD), dead trees, logs

1994 1995 1996	(Krankina & Harmon, 1995)	Boreal forest	Dynamics of dead wood in different successional stage forests that also vary in disturbance.	FM	C	Thinning and wood salvage (through forest management) reduces dead wood C stores drastically lower than their potential levels found in undisturbed forests. Natural disturbance increases dead wood C pool by a factor of 2-4.	204	Dead wood, windthrow, logs, snags, stumps
1997 1998 1999	(Delaney *et al.*, 1998)	All forest types	Comparison of quantity, decay stage and turnover of dead wood in three contrasting forest types (separated by climatic and physical zones).	FM	C	Dead wood quantity differed across the three climatic zones; lowest = dry, peak = moist, decreased slightly = wet. Decay stage in all three was mostly rotten or intermediate - very little woody debris was recent and intact. Overall no clear trend in turnover across the three climatic zones.	194	Dead wood, woody debris, downed wood, standing dead
2000 2001 2002	(Chambers *et al.*, 2000)	Tropical forest	Providing carbon cycling models with useful parameterisation and validation information for	FM	C	Uprooting and dead standing = the most common causes of tree mortality. Decomposition rate constants for trees killed by other falling trees were higher because trees killed by treefalls were on	279	Boles, coarse surface litter, dead trees

			coarse litter. Decomposition of boles.			average smaller than trees that died from other causes.		
2003 2004 2005	(Laiho & Prescott, 2004)	Conifer forest	The role of coarse woody debris in nutrient cycling.	R	P	Although CWD accounts for over 50% of organic matter, it contributes substantially small amounts of nutrients (N, P, K, Ca, Mg). CWD is of minor importance in the nutrient cycles of these forests.	225	Coarse woody debris (CWD)
2006 2007 2008	(Zielonka, 2006)	Sub-alpine spruce forest	Determined how long it took for a stem/fallen debris to be used as a substrate for recruitment.	FM	C	Although CWD covered only 4% of the forest floor, it accounted for over 40% of sapling stems. Highest recruitment on a log is generally between 30-60yrs which represents a decay state of between 4 & 7. But early colonisation is possible, but the slow decay can sometimes lead to slower growth of seedlings.	74	Dead wood, decaying wood, coarse woody debris (CWD), logs

2009 2010 2011	(Müller & Bütler, 2010)	European forests	Examining dead wood thresholds in forests for sustainable forest management.	R	P	Thresholds vary among studies with different species, habitats and regions. Provides baseline CWD thresholds for management decisions.	162	Dead wood, management, threshold
2012 2013 2014	(Dunn & Bailey, 2012)	Mixed conifer forests	Assessing the hypothesis that snags decay slower than logs, making the long term dynamics of seral forests dependent on snag fall decay and breakage.	FM	C	Confirmed hypothesis = reduced decay rates in stags and variation among species. Found variation in fall, breakage and decay among species and size = suggests increased diversity of snag species in number and size would meet the ecological needs of this forest type.	12	Coarse wood, coarse woody detritus (CWD), snags, logs
2015 2016	(Checko *et al.*, 2015)	Mixed deciduous forest	Importance of deadwood as a habitat for organisms and plants.	FM	C	49 vascular plant species colonised downed wood and these species were mostly small-seeded rather than heavier seeded plants. Abundance of species and organisms increased with greater logs sizes and decomposition. Deadwood served as a seed filter, capturing small seeds in cracks,	1	Coarse woody debris (CWD), deadwood, downed logs, logs

						where bigger seeds generally tended to roll off.		
CHARACTERISTICS ***Non-living & Structural Elements***								
1985 1986 1987	(King, 1986)	Maple forest	Investigation of the attributes that contribute to the susceptibility of *Acer saccharum* to wind damage.	FM	C	Larger trees are more susceptible to wind effects due to the loss of trunk/stem flexibility - this is also compounded by their increased exposure to wind as they grow taller (out of canopy).	169	Trees, trunk, canopy gaps
1988 1989 1990	(Maser *et al.*, 1988)	Pacific Northwest forests	How does the living and dead forest interact, what we know about the large trees that fall, and what are the implications of our management practices.	R	P	Snags are important structural components of a forest, and when fall, can cause different effects than a green tree that falls. Future forests will contain less CWD, and that CWD will be substantially smaller than we see today. Fallen trees add a different dimension to forests.	181	Fallen trees, coarse woody debris (CWD)

1991 1992 1993	(Kellman & Tackaberry, 1993)	Tropical riparian forests	Comparison of tree species distribution in two different areas that are especially prone to fire and tree fall.	FM	C	Tree fall was concentrated on upper valley slopes and tended to fall down slope. Fire-scarred trees were predominately found on gentler slopes. Both disturbances were determined to be important role in promoting species co-existence; providing a varied micro-climate for establishment, but patchy enough to ensure the disturbance-sensitive species continue to persist.	56	Tree falls, tree death
1994 1995 1996	(McCarthy & Bailey, 1994)	Hardwood forest	Investigated how management influences the distribution and abundance of CWD in the central Appalachians.	FM	C	Young stands had the highest density, volume and biomass of CWD. Following clear-cutting most CWD existed as relatively labile, low decay state, small-diameter. Crushed logs do not function ecologically in the same capacity as large intact logs.	153	Coarse woody debris (CWD), Standing snags, logs, stumps

1997 1998 1999	(Sturtevant *et al.*, 1997)	Boreal forest	Assessment of CWD abundance and structure for the purpose of comparing the differences across stand age & developing a model that predicts CWD availability, specifically for wildlife.	FM	C	Wind and insect defoliation strongly influence CWD accumulation. Size and relative density of standing trees are related to the susceptibility of individual trees to windthrow - and larger more isolated trees are increasingly vulnerable. Older stands are more prone to insect defoliation. CWD size is a function of standing tree size - CWD is influenced by site quality.	287	Coarse woody debris (CWD), fallen tree boles, downed wood, snag (standing dead wood)
2000 2001 2002	(Waddell, 2002)	Multiple forest types	Information on CWD is in-demand for wildlife biologists, fire specialists and ecologists most especially as an indicator of forest health - this paper explores the methods used to estimate CWD structural attributes.	R	P	Define an attribute of CWD as "any item or characteristic of the CWD population that a researcher or manager is interested in estimating…" This may include volume, log number, biomass and carbon. At a population level, these attributes are important for forest process and function including decomposition rates, accumulation, disturbance indicators.	152	Down wood, dead wood, coarse woody debris (CWD)

2003 2004 2005	(McElhinny *et al.*, 2005)	Multiple forest types	Review of the literature that has been associated with forest and woodland structural attributes and complexity.	R	P	No definitive suite of structural attributes for forests. Most common structural attributes that are presented in the literature: foliage arrangement, canopy cover, tree diameter, height, tree spacing, species, stand biomass understory vegetation and deadwood. To quantify logs the most useful attributes were abundance of large logs and variation in log number and size.	333	Logs, stags, standing dead trees, dead wood
2006 2007 2008	(Brassard & Chen, 2008)	Boreal forest	Characterisation of the volume and attributes of CWD in managed and unmanaged boreal forests.	FM	C	Following a fire disturbance stand age matters for CWD accumulation. Further, CWD dynamics differed with stand origin (logging).	56	Snags, coarse woody debris (CWD)
2009 2010 2011	(Ferry *et al.*, 2010)	Tropical forest	The role of topography, soil, tree growth and mortality in explaining variability in forest biomass at local scales.	FM	C	Along a topographic gradient there were higher rates of treefall, which decreased total stand basal area and favoured allocation to height growth and recruitment of light-demanding species with low	71	Treefall, woody biomass, topography,

						density. Highlights importance of including site characteristics in biomass measurements.		mortality, wood density
2012 2013 2014	(Asner & Levick, 2012)	Savanna	Influence of herbivores (elephants) on treefall.	FM	P	Elephants were revealed to be the primary agent of treefall, regardless of savanna condition.	50	herbivores, treefall dynamics, turnover
2015 2016	(Ganey *et al.*, 2015)	Mixed-conifer & pine forests	Assessments of log and snag density to inform policy and development of predictive models - comparing across two forest types.	FM/M	C	Human access to forests and management history has a large influence on large snag density - this is not accounted for in the management guidelines.	1	Snags, standing dead trees, fallen logs, logs, management
APPLICATION ***Modelling & Forest Management***								
1985 1986 1987	(Leemans & Prentice, 1987)	*Picea-Pinus* forest	Using a simulation model (FORSKA) to test the hypothesis that height and diameter distributions of the	M	C	The simulation generated a stand description similar to the real forest stand including the essential characteristics. Gap-models are important for simulating forest	107	Gap model, storm-felling

			trees are the outcome of storm-felling.			dynamics - the one used here is just one example.		
1988 1989 1990	(Ryan *et al.*, 1988)	Douglas-fir forest	Modelling the long term mortality of trees as a function of morphological variables such as diameter at breast height, season burnt, scorch height etc.	M	C	The best predictor of mortality was the number of quadrats with dead cambium. Percentage of crown volume scorched was a better predictor of mortality than lethal scorch height.	111	Models, Mortality, fire, bole damage, cambium
1991 1992 1993	(Bossel, 1991)	All forest types	Comparisons between explanatory and descriptive models for forest dynamics.	M	C	Recent software developments have increased our ability to use explanatory (simulation) models to examine forest dynamics - these enable us to cope with, and better predict changing environmental and management conditions.	89	Modelling, gaps, wood biomass

1994 1995 1996	(Pinard & Putz, 1996)	Diptero carp forest	Examining the effect of different logging methods on carbon (biomass).	FM/MM	C	41% of unharvested trees were damaged due to felling (uprooted and crushed) using the conventional method. When using a reduced-impact method 15% of trees were damaged - this means more carbon retention. Mortality of damaged trees may contribute to net decreases in biomass many years after logging.	416	Mortality, damaged trees, logging, tree felling
1997 1998 1999	(Krankina *et al.*, 1999)	Boreal forest	Exploring what happens to nutrients during woody decay, and what is the role of CWD in different successional stages.	M	C	Nutrient stores declined with decay state, and the rate of these losses were related to patterns of bark loss. Modelling revealed that post-disturbance release of nutrients from woody detritus can potentially supply a large proportion of nutrient accumulation in living biomass.	136	Woody detritus, decomposition, dead trees, decay, coarse woody debris (CWD)

2000 2001 2002	(Hartley, 2002)	All forest types	Provides a broad array of management recommendations.	R/M M	E	Lack of standing snags and fallen logs is the most obvious difference between planted and natural forests. Management is general and can apply to many regions. Suggests a new plantation forest paradigm based on the hypothesis that minor improvements in design and management can improve biodiversity outcomes while retaining economic benefit.	52 6	Plantations, harvesting, management, coarse woody debris (CWD)
2000 2001 2002	(Porté & Bartelink, 2002)	All forest types	Provide an overview of models designed for modelling tree dynamics, and review their suitability based on their intended use.	R/M	E	Suggest that in complex forest systems, tree-level models will be necessary to account for competition effects etc. These tree-to-tree interactions are necessary to provide reliable estimates of stand development.	26 9	Management, gap models, tree fall

2003 2004 2005	(Jonsson *et al.*, 2005)	Fennoscandia forests	Review of the organisms that are dependent on dead wood, and identify the challenges of their management.	R/MM	L	New approaches to management are called for! Argue that it is necessary to counteract the current shortage of dead wood, minimise isolation and edge effects by planning at the landscape level, create a variety of dead wood types to maximise biodiversity and habitats.	292	Dead wood, management, coarse woody debris (CWD)
2006 2007 2008	(Vanderwel *et al.*, 2006)	Boreal forest	Parameterisation of CWD decay-class models to better represent decomposition-related changes in snags and downed woody debris (DWD) over time.	M	C	DWD from trees that fell at death was projected to advance through 4 decay classes over a 55-60yr period, but those originating from stags was modelled to persist for up to 90yrs after tree death because of slower decomposition while standing. Diameter has a strong effect on DWD transitions into decay classes 2 & 4 but not 3.	51	Snag, downed woody debris, coarse woody debris (CWD), management, decay

2006 2007 2008	(Woodall & Monleon, 2008)	All forest types	Rationale and context of a national inventory of downed woody material for guiding management and providing data census.	R/M M	E	The DWM indicator can provide a good indication of forest health, and can provide information on DWM attributes that can be used across multiple forest ecosystems.	13 8	Downed woody materials (DWM), fine and coarse woody debris
2009 2010 2011	(Metcalf *et al.*, 2009)	Tropica l forest	How life expectancy and time to reach canopy (growth) interact to influence forest turnover.	R/M	C	Characterising the light environment (using an index of crown illumination) in integral projection modelling & age-from-stand analysis is important in capturing tree life history axis of movement through the light environment.	40	Turnover, mortality, crown illumination, gap
2012 2013 2014	(Mücke *et al.*, 2013)	All forest types	Presentation of a new method for the quantification of deadwood in forests.	M	P	Full waveform airborne laser scanning can be used as an important tool to accompany manual quantification of deadwood. Using a digital height model you can depict downed stems as line-like features.	14	Fallen trees, dead wood, downed trees

2015 2016	(Russell *et al.*, 2015)	All forest types	Critique of the methods used for quantifying dead wood with a predominate focus on biomass and carbon attributes.	R	E	A range of methods should be used when quantifying dead wood (C stores and fluxes) including detailed experiments that are region specific, to more general landscape protocol establishment. To date, there is no universal approach to determining the total amount of dead wood and its patterns of decomposition, but there are several approaches that will serve this purpose.	6	Dead wood, downed wood, coarse woody debris (CWD), standing dead

References

Aakala, T., Kuuluvainen, T., De Grandpre, L. & Gauthier, S. (2007) Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. *Canadian Journal of Forest Research*, **37**, 50-61.

Angers, V.A., Drapeau, P. & Bergeron, Y. (2010) Snag degradation pathways of four North American boreal tree species. *Forest Ecology and Management*, **259**, 246-256.

Asner, G.P. & Levick, S.R. (2012) Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters*, **15**, 1211-1217.

Bossel, H. (1991) Modelling forest dynamics - moving from description to explanation. *Forest Ecology and Management*, **42**, 129-142.

Brassard, B.W. & Chen, H.Y. (2008) Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. *Ecosystems*, **11**, 1078-1090.

Brokaw, N.V.L. (1987) Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology*, **75**, 9-19.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, **20**, 620-631.

Cannon, J.B., Barrett, M.E. & Peterson, C.J. (2015) The effect of species, size, failure mode, and fire-scarring on tree stability. *Forest Ecology and Management*, **356**, 196-203.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V. & Melack, J.M. (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380-388.

Checko, E., Jaroszewicz, B., Olejniczak, K. & Kwiatkowska-Falinska, A.J. (2015) The importance of coarse woody debris for vascular plants in temperate mixed deciduous forests. *Canadian Journal of Forest Research*, **45**, 1154-1163.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. (2005) Dead wood in European beech (Fagus sylvatica) forest reserves. *Forest Ecology and Management*, **210**, 267-282.

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A. & Quintero, N.B. (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica*, **30**, 2-11.

Denslow, J.S., Ellison, A.M. & Sanford, R.E. (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology*, **86**, 597-609.

Denslow, J.S., Schultz, J.C., Vitousek, P.M. & Strain, B.R. (1990) Growth responses of tropical shrubs to treefall gap environments. *Ecology*, **71**, 165-179.

Dunn, C.J. & Bailey, J.D. (2012) Temporal dynamics and decay of coarse wood in early seral habitats of dry-mixed conifer forests in Oregon's Eastern Cascades. *Forest Ecology and Management*, **276**, 71-81.

Ennos, A.R. (1997) Wind as an ecological factor. *Trends in Ecology & Evolution*, **12**, 108-111.

Esseen, P.-A. (1994) Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation*, **68**, 19-28.

Everham, E.M. & Brokaw, N.V.L. (1996) Forest damage and recovery from catastrophic wind. *The Botanical Review*, **62**, 113-185.

Ferry, B., Morneau, F., Bontemps, J.D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106-116.

Forrester, J.A., Mladenoff, D.J., Gower, S.T. & Stoffel, J.L. (2012) Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. *Forest Ecology and Management*, **265**, 124-132.

Fulé, P.Z., Cocke, A.E., Heinlein, T.A. & Covington, W.W. (2004) Effects of an intense prescribed forest fire: Is it ecological restoration? *Restoration Ecology*, **12**, 220-230.

Galhidy, L., Mihok, B., Hagyo, A., Rajkai, K. & Standovar, T. (2006) Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology*, **183**, 133-145.

Ganey, J.L., Bird, B.J., Baggett, L.S. & Jenness, J.S. (2015) Density of large snags and logs in northern Arizona mixed-conifer and ponderosa pine forests. *Forest Science*, **61**, 353-362.

Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2010) Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. *Oikos*, **119**, 475-484.

Greene, S.E., Harcombe, P.A., Harmon, M.E. & Spycher, G. (1992) Patterns of growth, mortality and biomass change in a coastal *Picea sitchensis - Tsuga heterophylla* forest. *Journal of Vegetation Science*, **3**, 697-706.

Guby, N.A.B. & Dobbertin, M. (1996) Quantitative estimates of coarse woody debris and standing dead trees in selected Swiss forests. *Global Ecology and Biogeography Letters*, **5**, 327-341.

Harmon, M.E. & Franklin, J.F. (1989) Tree seedlings on logs in *Picae-Tsuga* forests of Oregon and Washington. *Ecology*, 48-59.

Harmon, M.E. & Hua, C. (1991) Coarse woody debris dynamics in two old-growth ecosystems. *BioScience*, **41**, 604-610.

Hartley, M.J. (2002) Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management*, **155**, 81-95.

He, F.L. & Duncan, R.P. (2000) Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology*, **88**, 676-688.

Holzwarth, F., Kahl, A., Bauhus, J. & Wirth, C. (2013) Many ways to die–partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *Journal of Ecology*, **101**, 220-230.

Hunter, M.O., Keller, M., Morton, D., Cook, B., Lefsky, M., Ducey, M., Saleska, S., de Oliveira Jr, R.C. & Schietti, J. (2015) Structural dynamics of tropical moist forest gaps. *PloS ONE*, **10**, e0132144.

Jonsson, B.G. & Dynesius, M. (1993) Uprooting in boreal spruce forests - long-term variation in disturbance rate. *Canadian Journal of Forest Research*, **23**, 2383-2388.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005) Ecology of species living on dead wood–lessons for dead wood management. *Silva Fennica*, **39**, 289-309.

Kellman, M. & Tackaberry, R. (1993) Disturbance and tree species coexistence in tropical riparian forest fragments. *Global Ecology and Biogeography Letters*, 1-9.

King, D.A. (1986) Tree form, height growth, and susceptibility to wind damage in *Acer saccharum*. *Ecology*, 980-990.

Kirby, K.J., Reid, C.M., Thomas, R.C. & Goldsmith, F.B. (1998) Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology*, **35**, 148-155.

Kramer, M.G., Hansen, A.J., Taper, M.L. & Kissinger, E.J. (2001) Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology*, **82**, 2749-2768.

Krankina, O.N. & Harmon, M.E. (1995) Dynamics of the Dead Wood Carbon Pool in Northwestern Russian Boreal Forests. *Boreal Forests and Global Change: Peer-reviewed manuscripts selected from the International Boreal Forest Research Association Conference, held in Saskatoon, Saskatchewan, Canada, September 25–30, 1994* (ed. by M.J. Apps, D.T. Price and J. Wisniewski), pp. 227-238. Springer Netherlands, Dordrecht.

Krankina, O.N., Harmon, M.E. & Griazkin, A.V. (1999) Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. *Canadian Journal of Forest Research*, **29**, 20-32.

Kuuluvainen, T. (1994) Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland - A review. *Annales Zoologici Fennici*, **31**, 35-51.

Laiho, R. & Prescott, C.E. (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forest Research*, **34**, 763-777.

Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A., Swanson, F.J., HilleRisLambers, J., Sprugel, D.G. & Franklin, J.F. (2015) Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology*, **11**, 2855-2861.

Leemans, R. & Prentice, I.C. (1987) Description and simulation of tree-layer composition and size distributions in a primeval *Picea-Pinus* forest *Vegetatio*, **69**, 147-156.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. (1985) Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *Journal of Ecology*, 915-924.

Maser, C., Tarrant, R.F., Trappe, J.M. & Franklin, J.F. (1988) From the forest to the sea: a story of fallen trees. In. Portland, Or.: Pacific Northwest Research Station, US Dept. of Agriculture, Forest Service

McCarthy, B.C. & Bailey, R.R. (1994) Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. *Canadian Journal of Forest Research*, **24**, 1317-1329.

McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2005) Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management*, **218**, 1-24.

Metcalf, C.J.E., McMahon, S.M. & Clark, J.S. (2009) Overcoming data sparseness and parametric constraints in modeling of tree mortality: A new nonparametric Bayesian model. *Canadian Journal of Forest Research*, **39**, 1677-1687.

Mitchell, S.J. (2012) Wind as a natural disturbance agent in forests: a synthesis. *Forestry*, **00**, 1-11.

Mücke, W., Deák, B., Schroiff, A., Hollaus, M. & Pfeifer, N. (2013) Detection of fallen trees in forested areas using small footprint airborne laser scanning data. *Canadian Journal of Remote Sensing*, **39**, S32-S40.

Müller, J. & Bütler, R. (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*, **129**, 981-992.

Peterson, C.J. & Pickett, S.T.A. (1991) Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. *Forest Ecology and Management*, **42**, 205-217.

Peterson, C.J., Carson, W.P., McCarthy, B.C. & Pickett, S.T.A. (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos*, **58**, 39-46.

Phillips, J.D. & Marion, D.A. (2006) Biomechanical effects of trees on soil and regolith: Beyond treethrow. *Annals of the Association of American Geographers*, **96**, 233-247.

Pinard, M.A. & Putz, F.E. (1996) Retaining forest biomass by reducing logging damage. *Biotropica*, 278-295.

Porté, A. & Bartelink, H. (2002) Modelling mixed forest growth: a review of models for forest management. *Ecological Modeling*, **150**, 141-188.

Rebertus, A.J. & Veblen, T.T. (1993) Structure and tree-fall gap dynamics of old-growth Nothofagus forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science*, **4**, 641-654.

Rich, R.L., Frelich, L.E. & Reich, P.B. (2007) Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. *Journal of Ecology*, **95**, 1261-1273.

Ritter, E., Dalsgaard, L. & Einhorn, K.S. (2005) Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *Forest Ecology and Management*, **206**, 15-33.

Russell, M.B., Fraver, S., Aakala, T., Gove, J.H., Woodall, C.W., D'Amato, A.W. & Ducey, M.J. (2015) Quantifying carbon stores and decomposition in dead wood: A review. *Forest Ecology and Management*, **350**, 107-128.

Ryan, K.C., Peterson, D.L. & Reinhardt, E.D. (1988) Modeling long-term fire-caused mortality of Douglas-fir. *Forest Science*, **34**, 190-199.

Samonil, P., Antolik, L., Svoboda, M. & Adam, D. (2009) Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. *Forest Ecology and Management*, **257**, 1148-1156.

Schaetzl, R.J., Johnson, D.L., Burns, S.F. & Small, T.W. (1989) Tree uprooting - Review of terminology, process, and environmental implications. *Canadian Journal of Forest Research*, **19**, 1-11.

Schnitzer, S.A. & Carson, W.P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, **82**, 913-919.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D. & Spycher, G. (1987) Patterns of log decay in old-growth Douglas-fir forests. *Canadian Journal of Forest Research*, **17**, 1585-1595.

Sturtevant, B.R., Bissonette, J.A., Long, J.N. & Roberts, D.W. (1997) Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecological Applications*, **7**, 702-712.

Tritton, L.M. & Siccama, T.G. (1990) What proportion of standing trees in forests of the northeast are dead? *Bulletin of the Torrey Botanical Club*, **117**, 163-166.

Vanderwel, M.C., Malcolm, J.R. & Smith, S.M. (2006) An integrated model for snag and downed woody debris decay class transitions. *Forest Ecology and Management*, **234**, 48-59.

Waddell, K.L. (2002) Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecological Indicators*, **1**, 139-153.

Whitmore, T. (1989) Canopy gaps and the two major groups of forest trees. *Ecology*, **70**, 536-538.

Woodall, C.W. & Monleon, V.J. (2008) Sampling protocol, estimation, and analysis procedures for the down woody materials indicator of the FIA program. *General Technical Report - Northern Research Station, USDA Forest Service*, 68 pp.-68 pp.

Zielonka, T. (2006) When does dead wood turn into a substrate for spruce replacement?

Journal of Vegetation Science, **17**, 739-746.

Appendix 4

Chapter VI: READING THE FOREST LOGBOOK: ENVIRONMENTAL DRIVERS OF LIVING AND DEAD ELEMENTS OF AUSTRALIAN EUCALYPT FORESTS

Table Appendix 4: Summary of the models testing the importance of the following predictors of predictors of (i) basal area of living trees (BA_{LIVING}) and (ii) quantity of course woody debris (CWD): slope (degrees), aspect (cardinal direction), ferns (presence/absence), clumping grass (presence/absence), woody seedlings (presence/absence), bare ground (presence/absence), and shrubs (presence/absence).

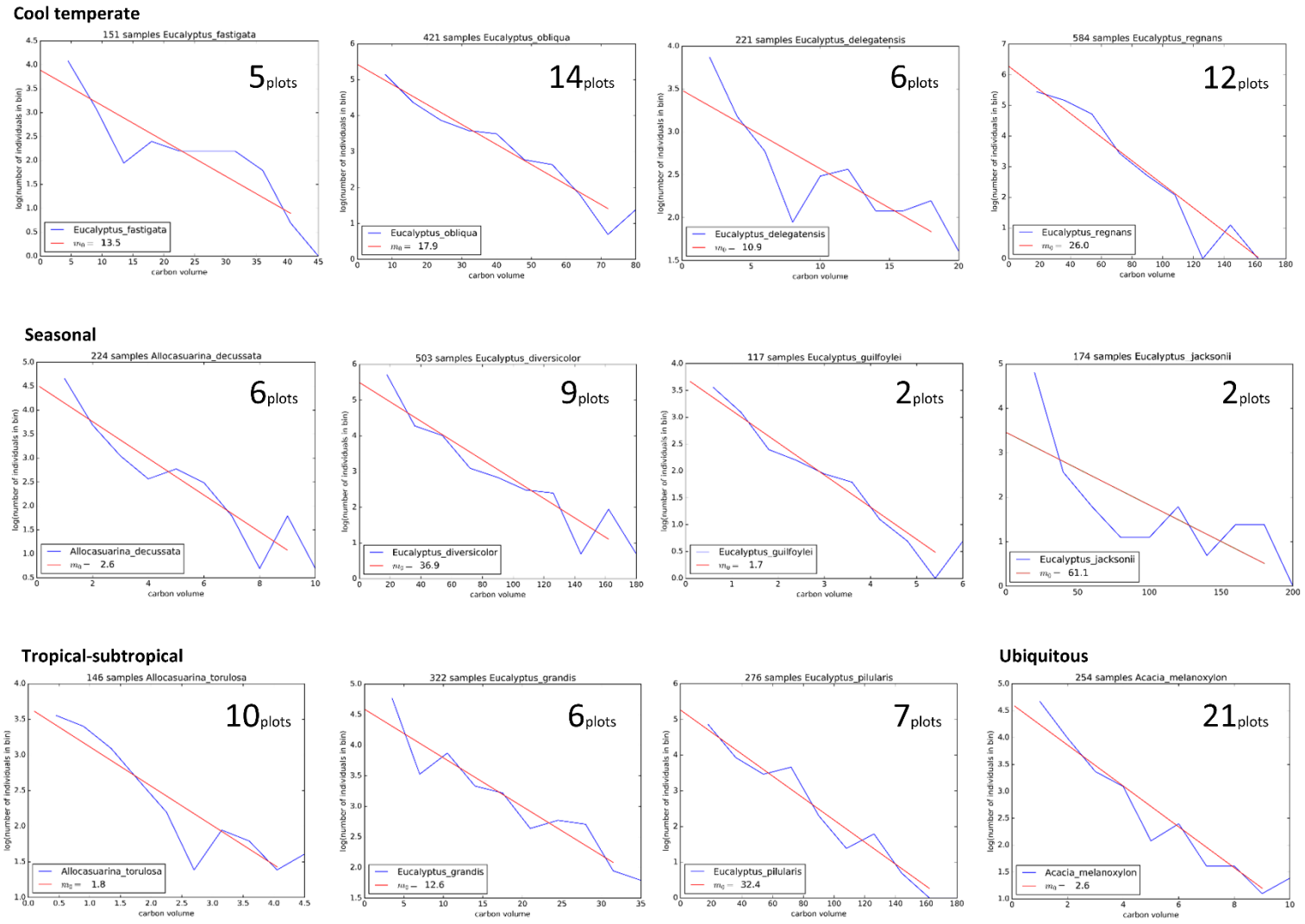
ID	Plot ID	No.Live	No.standingdead	No.species.live	No.euc.sp.live	No.sticks	No.logs	BA.Living	BA.logs	MAT	MAP.C
1	T.BT	496	84	13	2	368	64	73.76	1119.58	10.3	245.25
2	T.WR	616	118	12	1	480	82	72.6	1122.25	11.2	143.25
3	T.ZZ	1028	137	9	2	693	71	91.21	1195.47	10.2	160.25
4	T.MF	677	108	13	4	966	187	99.87	1008.88	6.6	88.25
5	T.WD	288	66	10	2	269	51	40.42	474.921	11	7.25
6	T.SX	473	82	11	2	375	91	76.85	1285.91	9.7	78.25

7	W.CA	114	13	3	2	432	62	52.48	494.308	15.3	-122.75
8	W.CL	110	4	4	3	305	63	116.75	479.962	15	-16.75
9	W.DW	165	38	4	2	428	39	34.49	349.668	15.2	-115.75
10	W.FR	192	3	4	2	276	53	48.1	432.645	14.8	-194.75
11	W.SU	253	46	4	2	283	53	42.06	311.87	15	-214.75
12	W.DK	292	20	5	2	482	60	63.08	421.926	15.2	-57.75

ID	Plot ID	Av.Slope	Aspect	Elev	Rock	BareG	Ferns	wseedling	carpet.grass	clump.grass	shrubs
1	T.BT	0.26364	S	212	0	1	1	1	0	1	0
2	T.WR	0.02332	S	111	0	1	1	1	0	1	0
3	T.ZZ	0.20867	N	284	1	1	1	0	0	1	0
4	T.MF	0.19116	S	843	1	0	1	0	0	1	1
5	T.WD	0.14324	S	87	1	0	1	0	0	0	0
6	T.SX	0.13265	S	560	1	0	1	0	0	0	1
7	W.CA	0.12784	S	164	0	1	1	0	1	0	0
8	W.CL	0.16334	N	165	0	0	1	1	0	1	1
9	W.DW	0.11026	N	148	0	0	0	1	1	0	1

10	W.FR	0.24918	S	239	1	0	0	1	0	0	1
11	W.SU	0.14908	N	142	0	1	1	1	1	0	1
12	W.DK	0.14592	S	93	0	0	1	0	1	1	1

Distribution of volume by size classes.



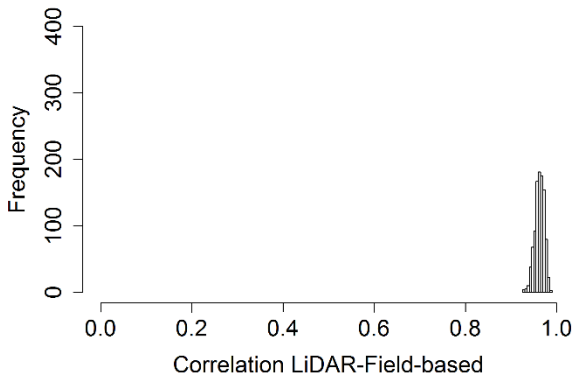
Relationship between biomass and the number of individuals, plotted for each eucalypt species with more than 100 individuals across the 48 one-hectare Ausplots. Most species show a log-linear relationship between the of the number of individuals and the volume of carbon, with the exception of *Eucalyptus delegatensis* and *E. jacksonii* (with an excess of small individuals).

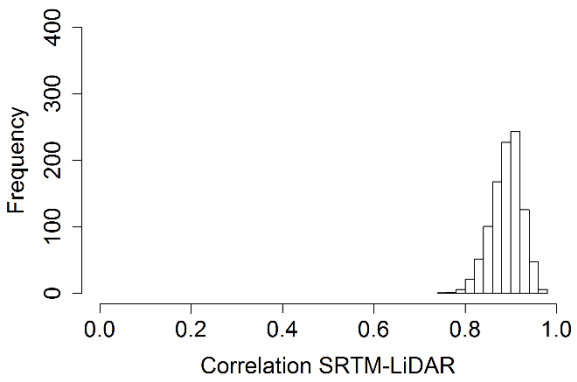
Appendix 5

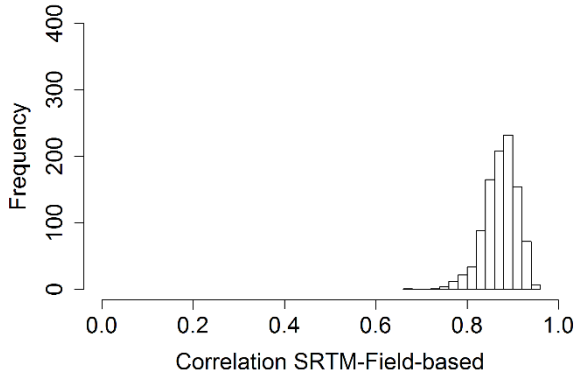
Chapter VIII: A PRACTICAL METHOD FOR CREATING A DIGITAL TOPOGRAPHIC SURFACE FOR ECOLOGICAL PLOTS USING GROUND-BASED MEASUREMENTS

Frequency distribution of the correlation coefficient for each pair of comparisons (LiDAR-Field, LiDAR-SRTM, SRTM-field), calculated for a) North Styx, b) Bird Track, c) Mount Field, and d) Weld River.

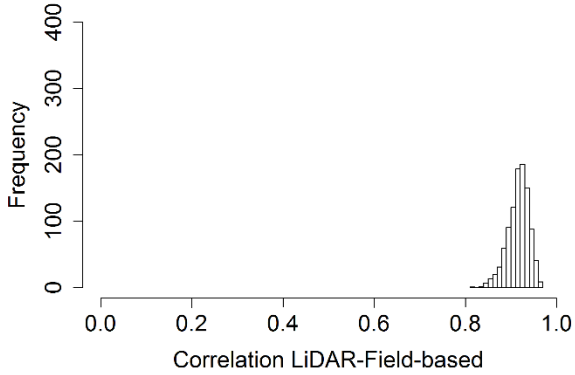
a) North Styx

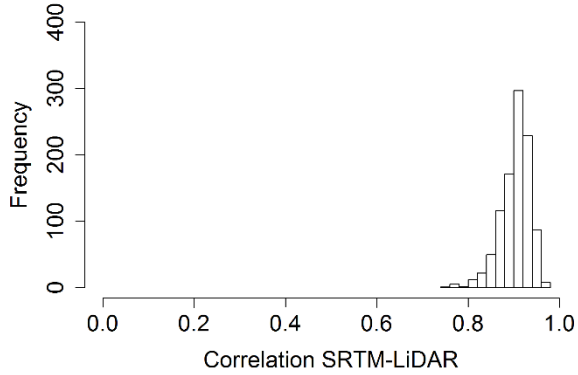


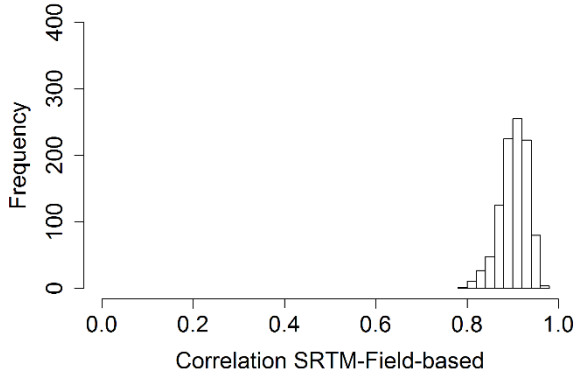




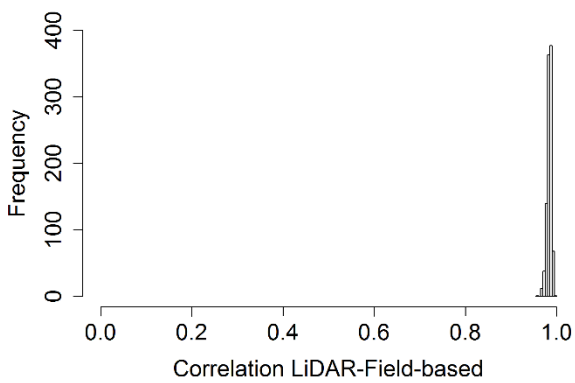
b) Bird Track

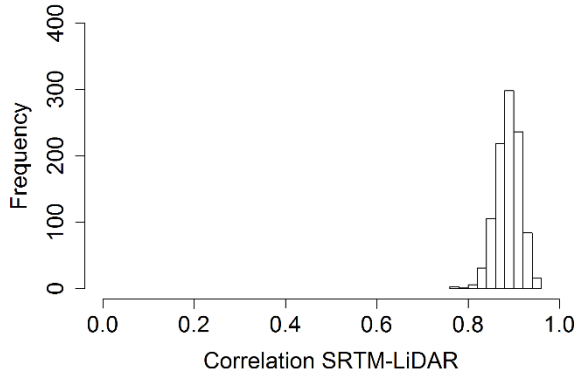


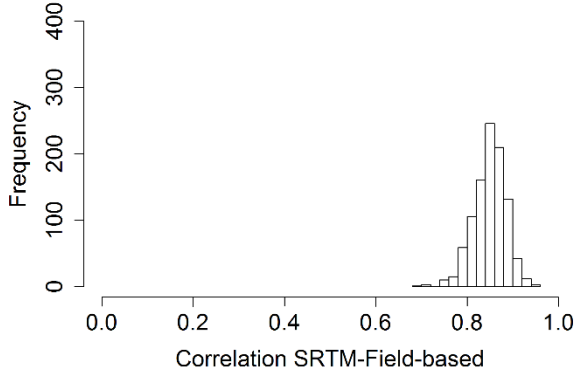




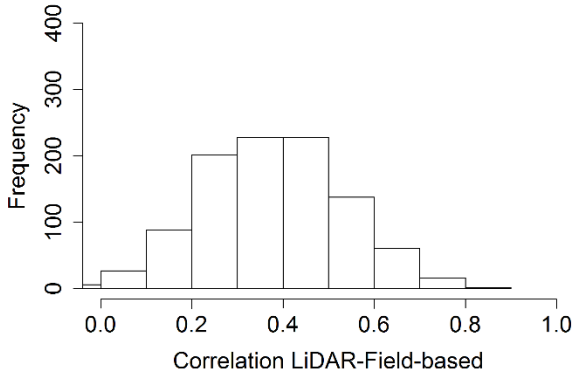
c) Mount Field







d) Weld River


Frequency
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0.0
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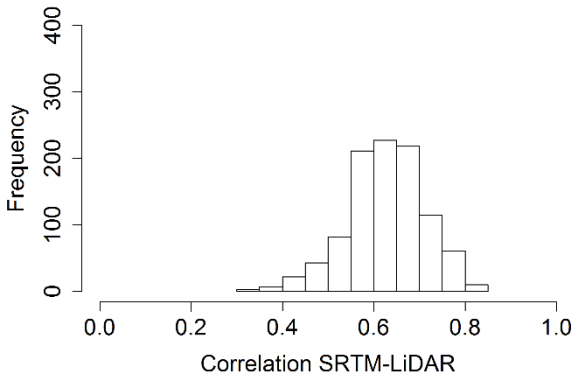
0.8
1.0
Correlation LiDAR-Field-based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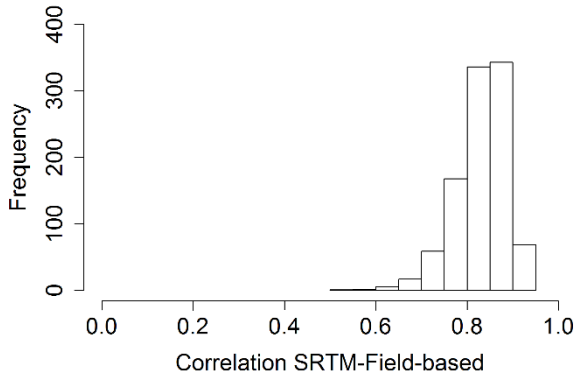
Correlation SRTM-LiDAR


Frequency
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Correlation SRTM-Field-based

Appendix 6

Chapter IX: MODELLING LINEAR SPATIAL FEATURES IN ECOLOGY

Figure captions

Figure S1. The vector alignment parameter, $\vec{v} \cdot \vec{\nabla} h$, as a function of slope, $|\vec{\nabla} h|$. The triangular distribution comes from the linear proportionality of *y* on *x*. The *y* scale is in metres, the *x* scale is dimensionless. The black line joins the mean values of *y* for four subsets of the points, with equal quartiles of 208 logs each, as indicated by different colour points. Since $\langle \vec{v_i} \cdot \vec{\nabla} h \rangle$ depends linearly on $|\vec{\nabla} h|$, the points on the figure are distributed in a triangle pattern (the individual logs are plotted as points). Note that the *x* axis is dimensionless, with $|\vec{\nabla} h|$ * 100 sometimes called the percent grade. There is a clear downward curvature with increasing *x*.

Figure S2. The unit vector alignment parameter, $(\hat{u} \cdot \vec{\nabla} h)$. In this case the lengths of the logs are not considered, and each log becomes a unit vector with direction information only.

Table S1 – Vector sums for logs in 12 one-hectare forest plots from Australia.

plot	n	$\langle \sum \vec{v}_x \rangle$	$\langle \sum \vec{v}_y \rangle$	σ_v	$\lvert \sum \vec{v} \rvert \,/\, \sigma_v$	$\sum \vec{u}_x$	$\sum \vec{u}_y$	σ_u	$\lvert \sum \hat{u} \rvert \,/\, \sigma_u$
T-BT	64	+2.98	-6.25	2.48	2.79	+11.81	-21.04	8.00	3.02
T-ZZ	70	-3.75	-9.75	2.55	4.10	-10.56	-30.95	8.37	3.91
W-FR	53	-3.53	+5.19	1.65	3.82	-8.70	+20.16	7.28	3.02
T-WD	51	-0.24	-4.44	2.20	2.02	+0.05	-13.48	7.14	1.89
W-CL	63	+3.44	+3.29	1.48	3.21	+17.09	+14.05	7.94	2.79
T-MF	187	+3.45	-0.53	1.00	3.51	+53.04	-3.55	13.67	3.89
W-DW	39	+4.73	+3.86	2.20	2.77	+13.79	+12.43	6.24	2.97
W-DK	60	-0.60	-1.24	1.62	0.85	-5.26	-4.45	7.75	0.89
W-SU	52	-4.38	+1.28	1.89	2.41	-14.38	+2.90	7.21	2.03
T-SX	91	+0.98	-0.28	1.88	0.54	-0.56	+2.63	9.54	0.28
T-WR	82	+0.98	+4.82	2.01	2.45	-1.32	+18.69	9.06	2.07
W-CA	61	-0.47	-0.32	1.95	0.29	-2.88	-0.35	7.81	0.37

Figure S2:

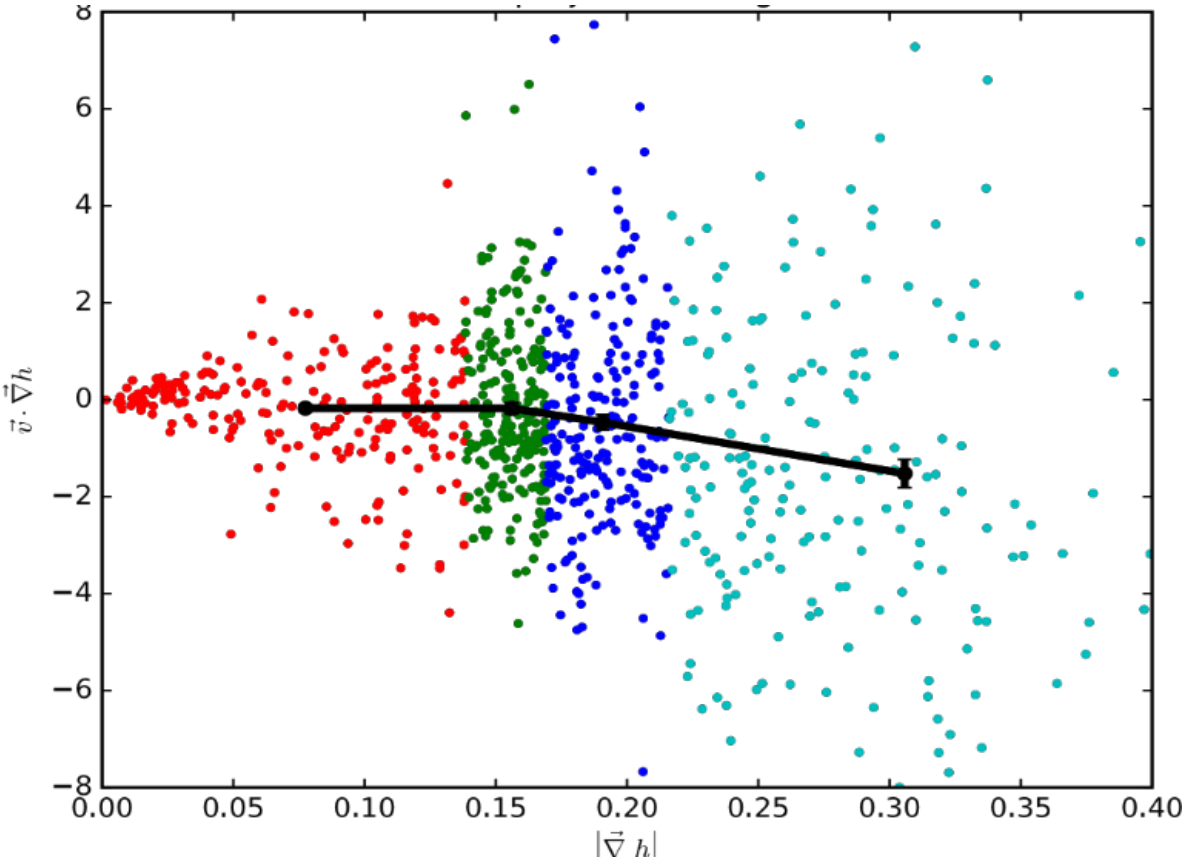
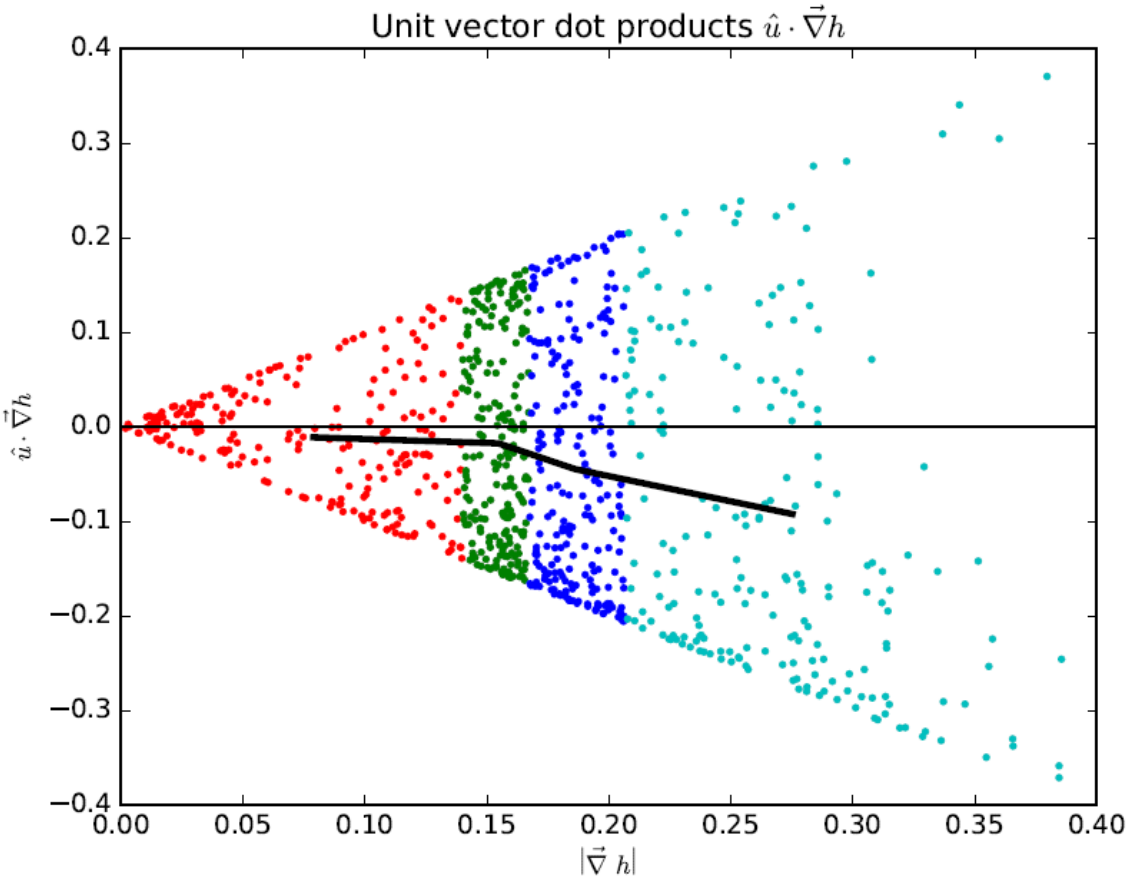

8
6
4
2
0
−2
−4
−6
−8
$\vec{v} \cdot \vec{\nabla} h$
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
$|\vec{\nabla} h|$

Figure S3:


Unit vector dot products $\hat{u} \cdot \vec{\nabla} h$
0.4
0.3
0.2
0.1
0.0
−0.1
−0.2
−0.3
−0.4
$\hat{u} \cdot \vec{\nabla} h$
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
$|\vec{\nabla}\ h|$